Land-use mediated effects on communities and single species of herbivorous insects

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Für die Käfersammler und Tiefseetaucher Lukas und Jonas

und meinen Opa

Probleme kann man niemals mit derselben Denkweise lösen,
mit der sie entstanden sind.

Albert Einstein

CONTENTS

SUMMARY

Anthropogenic land use is an established driver of biodiversity loss. The complexity and far-reaching consequences of land-use effects needs broad and intensive research. Besides small-scale studies, which are important to focus upon habitats, large-scale studies are essential to fully examine global implications of anthropogenic land-use.

The present study comprises both small- and large-scale investigations aiming to understand the impacts of land-use intensity on herbivorous insects in grassland ecosystems. The goal of the study was to understand the effects of intensified land-use on 1) whole communities, 2) single species, and 3) to understand the direct effects of resource-fertilization on herbivores.

The first and second research chapters examine the effects of compound land-use intensity and its three management types fertilization, mowing and grazing on Orthoptera, and Auchenorrhyncha (plant- and leafhoppers) community as well as single-species responses. Both groups are important insect-herbivores covering two major feeding guilds: leaf chewers (Orthoptera) and sap suckers (Auchenorrhyncha). To cover a broad gradient of land-use intensity defined by fertilization, mowing and grazing intensity, 150 grassland sites have been sampled. The studies were part of the Biodiversity Exploratories: a German-wide long-term project investigating land-use effects on biodiversity and ecosystems.

In chapter I, the effects of land-use intensity on diversity and abundance of Orthoptera were evaluated. In addition to my own intensive sampling in 2014, the data of a six-years sampling period (2008 – 2013) has been considered. We found diversity declines of Orthoptera with increasing compound land-use intensity, fertilization, mowing and grazing intensity. Abundance declined with increased mowing and grazing intensity, but was not affected by compound land-use and fertilization. The longer the time period after the last mowing date, the higher were diversity and abundance. Additionally we calculated a land-use niche for each Orthoptera species, which reflects the main occurrence of this species along the land-use gradient and gives insight into its susceptibility to land use. Comparing the species distribution with an expected distribution based on a randomization approach, we characterized 'losers' and 'winners' of high land-use intensity. The niche model detected half of the species as losers of intensive land-use and only three winners. Fertilization was the most detrimental management type on the species level, as we found no winners and many losers, followed by mowing and grazing.

In chapter II we examined land-use effects on α- and β-diversity of Auchenorrhyncha communities. While α-diversity comprises species richness of the sites, β-diversity describes the differences in community composition between sites. In our study we sampled 140 grassland sites by collecting Auchenorrhyncha of five randomly chosen plots of 1 m^2 each within the sites. This sampling method allowed us to both gather density/m^2 and obtain five different communities within the sites. The latter enabled us to describe land-use effects on β-diversity within the sites by comparing the differences in

community composition and species turnover among the five plots. We found decreasing β-diversity with increasing compound land-use intensity, that is, communities within sites become more homogenous with increasing land-use. Species richness as well as density of Auchenorrhyncha declined with compound land-use, fertilization and mowing intensity and were not affected by grazing. We also considered the species-specific view on the community with the above-described niche-model and found a high proportion of species being losers of high compound land-use intensity. Zooming into the management types, Auchenorrhyncha were, on the species level, mostly impaired by mowing, followed by fertilization and grazing intensity. Correspondingly, we found that dietary specialists decreased and generalists increased with increasing land-use intensity.

Chapter III presents direct fertilization-mediated resource-effects on grasshopper preference and performance. The study was conducted in the laboratory and the botanical garden where we grew orchardgrass with four different fertilization treatments. To simulate strong fertilization we applied N and NPK fertilizer (both with high nitrogen amount); weak fertilization was simulated with manure-fertilized grass; unfertilized grass was grown as control. In a choice experiment, we provided grasshoppers of different ages and species with each N, NPK and unfertilized grass. We found that the grasshoppers generally preferred highly fertilized grass, however, there were differences between nymphs and adults and between the species. In an additional no-choice experiment, we aimed to understand food and nutrient utilization of grasshoppers that had each only one of the four fertilization-treatments as food plant. We analysed performance, N and C content of grasshopper biomass and faeces. Grasshoppers of the different treatments did not differ in survival or consumption, but N- and NPK grasshoppers had increased N-concentration in their body mass, even though plant N-concentration did not differ between the treatments.

In summary, this thesis confirms the harmfulness of anthropogenic land-use on biodiversity. Both important representatives of the feeding guilds ‘leaf chewers’ and ‘sap suckers’ of insect-herbivores revealed diversity declines with an increase of land-use intensity. A few winning species replace a majority of losers of high land-use intensity and communities thus become more homogenous within managed sites. The harmfulness of fertilization that was demonstrated in chapter I and II might be rather mediated by indirect effects, such as loss of micro habitats, changes in micro climate and loss of food-plant species, than by direct resource-effects, as no fertilization-mediated differences in survival or consumption in the feeding experiments of chapter III were found. Loss of Auchenorrhyncha species is very likely mediated by loss of plant-diversity, as this group contains many dietary specialists. Loss of Orthoptera species is potentially caused by physical damage through agricultural machines and changes in vegetation and microhabitat structure. Annual changes in land-use intensity, a trend to moderate management and protection of surrounding habitats, could help to save our native grassland diversity. This thesis reveals the opportunity to gain a broad insight into the complex and various effects of land-use on biodiversity by giving attention to different levels of an ecosystem.

ZUSAMMENFASSUNG

Anthropogene Landnutzung ist eine bekannte Ursache für den Biodiversitätsverlust. Die Komplexität der weitreichenden Konsequenzen der Landnutzung verlangen nach breitgefächerter und intensiver Forschung. Neben kleinräumigen Studien, welche besonders wichtig sind, um sich auf Habitate zu fokussieren, sind großräumige Studien essentiell, um globale Folgen der Landnutzung vollständig zu erfassen.

Die vorliegende Arbeit umfasst sowohl kleinräumige als auch großräumige Studien, um die Einflüsse von Landnutzung auf herbivore Insekten in Grünlandökosystemen besser zu verstehen. Dabei ist das Ziel der Studie Landnutzungseffekte sowohl auf 1) Gesamtgemeinschaften und 2) einzelne Arten zu ergründen, als auch 3) die direkten Effekte von Pflanzendüngung auf herbivore Insekten zu verstehen.

Das erste Forschungskapitel befasst sich mit den Effekten von Landnutzungsintensität und den drei Bewirtschaftungstypen Düngung, Mahd und Beweidung, auf Orthoptera (Heuschrecken), das zweite Kapitel auf Auchenorrhyncha (Zikaden). Bei beiden Gruppen handelt es sich um wichtige Vertreter der herbivoren Insekten, wobei zwei der Haupt-Ernährungstypen abgedeckt werden: die blattfressenden (Orthoptera) und die pflanzensaftsaugenden (Auchenorrhyncha) Herbivoren. Um einen breiten Landnutzungsgradienten abzudecken, der durch die Intensität von Düngung, Mahd und Beweidung definiert wird, wurden 150 Grünlandflächen beprobt. Die Studien waren Teil der „Biodiversitäts-Exploratorien“: ein deutschlandweites Langzeitprojekt, das sich mit den Effekten von Landnutzung auf die Biodiversität und Ökosysteme befasst.

In Kapitel I werden die Effekte der Landnutzungsintensität auf die Diversität und Abundanz von Heuschrecken bewertet. Dazu wurden Daten aus meiner eigenen intensiven Sammelperiode im Jahr 2014 und zusätzlich die einer sechsjährigen Beprobung (2008 – 2013) berücksichtigt. Wir haben bei den Heuschrecken Diversitätsverluste durch steigende Gesamtlandnutzung und steigende Düngung, Mahd und Beweidungsintensität festgestellt. Die Abundanz verringerte sich mit steigender Mahdfrequenz und Beweidungsintensität, wurde aber nicht von der Gesamtlandnutzung und Düngeintensität beeinflusst. Je länger die Zeit nach der letzten Mahd war, desto höher waren sowohl die Diversität, als auch die Abundanz der Heuschrecken. Zusätzlich berechneten wir eine Landnutzungs-Nische für jede Art, welche das Hauptvorkommen der Art entlang des Landnutzungsgradienten widerspiegelt und die Empfindlichkeit der Art gegenüber Landnutzung aufdeckt. Durch einen Vergleich der Verbreitung einer Art entlang des Gradienten mit einem Erwartungswert, der auf einer Randomisierung basiert, konnten wir Verlierer und Gewinner von hoher Nutzungsintensität charakterisieren. Das Nischen-Modell konnte die Hälfte der Heuschreckenarten als Verlierer und nur drei Arten als Gewinner von starker Nutzungsintensität erfassen. Dabei war Düngung der schädlichste Bewirtschaftungstypen, gefolgt von Mahd und Beweidung.

In Kapitel II wurden die Effekte von Landnutzungsintensität auf die α- und β-Diversität von Zikadengemeinschaften untersucht. Während die α-Diversität die Artenzahl auf den Flächen beschreibt, geht es bei der β-Diversität um den Vergleich der Gemeinschaften zwischen Flächen. In unserer Studie haben wir 140 Grünlandflächen beprobt, indem wir alle Zikaden von fünf zufällig ausgewählten Plots zu je 1 m^2 aufgesammelt haben. Diese Sammelmethode erlaubte uns, sowohl die Dichte/m^2 als auch fünf verschiedene Gemeinschaften innerhalb jeder Fläche zu erfassen. Letzteres ermöglichte eine Untersuchung von Landnutzungseffekten auf die β-Diversität innerhalb der Flächen, indem die fünf Plots auf Unterschiede in der Zusammensetzung ihrer Gemeinschaft und der Artfluktuation geprüft wurden. Wir konnten einen Rückgang der β-Diversität mit steigender Gesamtlandnutzung feststellen. Die Artenzahl und die Dichte der Zikaden nahmen beide mit steigender Gesamtlandnutzung, Dünge- und Mahdintensität ab, wurden aber von Beweidung nicht beeinflusst. Auch die artspezifische Betrachtung der Zikadengemeinschaft wurde erfasst; dazu wurde das oben genannte Nischen-Modell verwendet. Ein Großteil der Arten waren Verlierer von starker Nutzungsintensität. Im Bezug auf die einzelnen Bewirtschaftungstypen waren die Zikaden am empfindlichsten gegen Mahd, gefolgt von Düngung und Beweidung. Dementsprechend stellten wir fest, dass der Anteil an Nahrungsspezialisten mit steigender Landnutzung abnahm und der von Nahrungsgeneralisten zunahm.

In Kapitel III werden die direkten Effekte gedüngter Pflanzen auf die Präferenz und Performanz von Heuschrecken präsentiert. Die Studie wurde im Labor und botanischen Garten durchgeführt, in welchem Wiesen-Knäuelgras kultiviert wurde, das vier verschiedenen Düngebehandlungen unterzogen wurde. Um eine starke Düngung zu simulieren wurde N und NPK-Dünger (beide in hohen Stickstoffkonzentrationen) ausgebracht; mäßige Düngung wurde durch Festmistdüngung simuliert; ungedüngtes Gras diente als Kontrolle. In einem Präferenz-Experiment, wurden Heuschrecken verschiedenen Alters und unterschiedlicher Art drei Grashalme (N, NPK, Kontrolle) angeboten. Wir fanden heraus, dass die Heuschrecken hauptsächlich stark gedüngtes Gras bevorzugten, es aber Unterschiede zwischen verschieden alten Tieren und den Arten gab. In einem anschließenden Performanz-Experiment, sollten die Unterschiede in Futter- und Nährstoffnutzung von Heuschrecken untersucht werden, die nur mit einer der vier Ressourcen (N, NPK, Kontrolle, Festmist) gefüttert wurden. Wir analysierten die Performanz und den N- und C-Gehalt der Körpermasse und der Fäzes. Die Heuschrecken der verschiedenen Behandlungsgruppen unterschieden sich nicht im Überleben oder im Futterkonsum, aber N- und NPK-Heuschrecken hatten einen höheren N-Gehalt in ihrer Körpermasse, obwohl die Pflanzen der verschiedenen Düngegruppen sich nicht im N-Gehalt unterschieden.

Zusammengefasst bestätigt diese Doktorarbeit die Schädlichkeit der anthropogenen Landnutzung für die Biodiversität. Beide Vertreter der wichtigen Herbivoren-Ernährungstypen „Blattfresser“ und „Pflanzensaftsauger“ zeigten Diversitätsverluste mit steigender Nutzungsintensität. Ein paar Gewinner-Arten ersetzen den großen Teil an Verlierer-Arten und dadurch werden die

Artgemeinschaften innerhalb der Flächen immer homogener. Die Schädlichkeit von Düngung die in Kapitel I und II aufgezeigt wurde, ist wahrscheinlich eher durch indirekte Effekte, wie den Verlust von Mikrohabitaten, der Veränderung des Mikroklimas und dem Verlust der Pflanzendiversität begründet, als durch direkte Ressourceneffekte; denn weder das Überleben noch der Konsum unterschied sich zwischen einzelnen Behandlungsgruppen im Futterexperiment aus Kapitel III. Der Verlust der Zikadendiversität ist wahrscheinlich durch den Pflanzendiversitätsverlust begründet, da diese Gruppe sehr viele Nahrungsspezialisten enthält. Der Verlust der Heuschreckendiversität ist potentiell durch physikalische Beeinträchtigung durch landwirtschaftliche Maschinen und die Veränderungen der Vegetations- und Mikrohabitatstruktur begründet. Jährliche Schwankungen in der Nutzungsintensität oder ein Trend zu moderaterer Bewirtschaftung und den Schutz umliegender Habitate, könnten helfen unsere heimische Grünland-Diversität zu schützen. Diese Doktorarbeit zeigt die Möglichkeit auf, einen breiten Einblick in die komplexen und unterschiedlichen Effekte der Landnutzung auf die Biodiversität zu erhalten, indem die unterschiedlichen Ebenen eines Ökosystems berücksichtigt werden.

GENERAL INTRODUCTION

Biodiversity crisis

Healthy ecosystems are not only important for biodiversity and ecosystem processes, but also for humanity. Ecosystems deliver services that humanity depends on. Ecosystem services such as water supply, food supply, gas regulation, pest control or pollination (Costanza et al. 1997) are processes and products of anthropogenic use. By contrast, ecosystem functions can be the same processes, but by definition are of ecosystem and earth-system use. Pollination for instance is as an ecosystem service important for human fruit supply and as an ecosystem function important for reproduction of plants. Human activities imperil the balance of ecosystems and their functions. The global nitrogen cycle for example, which is altered by several practices such as fertilization or fossil fuel combustion (Vitousek et al. 1997). Ecosystem functions can also suffer through an increase of species extinctions (Hooper et al. 2005, Dirzo et al. 2014) which increase through human impact.

The current biodiversity crisis is to a great extent caused by anthropogenic influences (Pimm et al. 1995, Hooper et al. 2005). Researchers from different countries have quantified 'planetary boundaries' (see Fig. 1.1) based on scientific knowledge, defining the space in which humanity can perform safely on our planet (Rockström et al. 2009). According to Rockström et al. (2009) the planetary boundary for species loss has already passed the limit, which has been reconfirmed in recent studies (Steffen et al. 2015). Biodiversity loss is not only disillusioning *per se*, but also subsequently affects other planetary boundaries, like water quality and hence global fresh water use (Rockström et al. 2009), and as mentioned above, can disturb ecosystem functions and thus human welfare.

Ecosystem stability is dependent on many different factors. The diversity of functional groups is one of these important factors (Tilman et al. 1997, McCann 2000). Functional diversity describes the various functions and traits that organisms hold in the ecosystem they inhabit. The complex network of many different interactions between diverse organisms and their environment is dependent on the variety of functions. A loss of species leads in turn to loss of ecosystem functionality (Dirzo et al. 2014). This loss of ecosystem functionality was reported for some groups of insects where functional diversity was positively related to species diversity (Birkhofer et al. 2015). Likewise forest ecosystems suffer from alterations like climate or land-use change through loss of biodiversity and functionality; species mixtures show higher productive output and less pest damage than monocultures (Bengtsson et al. 2000). Species diversity can also prevent outbreaks of single species or pests. In marine ecosystems overfishing and thus reduction of predators cause mass occurrence of jellyfish (Ghermandi et al. 2015). Cumulative effects like predator extinctions drive arthropod pests, which in turn lead to crop losses (Dirzo et al. 2014). Thus, the consequences of biodiversity loss are wide and scientists only superficially understand the impacts humanity will be confronted with.

Contribution of single species to an ecosystem

It is of great importance to study anthropogenic influences on whole communities as an ecosystem is built of numerous interactions. However, paying attention to individual species is of the same importance, as the loss of single species can have great impact on ecosystem stability, e.g. resistance against invasions (Lyons and Schwartz 2001). Of course there are sets of species that share their niche, or at least parts of it, in an ecosystem (i.e. they share their functional group), while others are irreplaceable. Species that have the same function in an ecosystem are called functionally redundant (Lawton and Brown 1994). The consequence of redundancy is called 'insurance hypothesis for biodiversity' and has been discussed multiple times by researchers (Tilman 1996, Folke et al. 1996, Naeem and Li 1997). The more species occupy a functional group, the better losses of single species within that functional group can be compensated by the ecosystem. This would happen through compensatory growth, that is, the gap that emerged through the loss or decrease of species A will be closed by increased growth of species B (Tilman 1996). But the significance of functional redundancy is controversial, as it implies the replaceability of single species. The loss of species in an ecosystem results in the loss of functional redundancy, and thus reduces ecosystem reliability (Naeem 1998).

Biodiversity loss and homogenization through anthropogenic land-use

The most important driver of diversity loss among anthropogenic practices is land-use intensification (Sala et al. 2000, Tilman et al. 2001), which is still increasing through the expanded need for natural resources by humans (Foley et al. 2005). In this context species loss is primarily driven by the loss of habitats and landscape fragmentation, but also by the introduction of exotic species, and soil or water degradation (Foley et al. 2005). Aquatic ecosystems and soils suffer from irrigation of agricultural land through salinization and nutrient enrichment (Tilman et al. 2001). Fragmentation through land use can trigger immediate extinctions in short-living organisms like butterflies or time-displaced species extinctions in longer living plants (Krauss et al. 2010).

Through land use, landscapes have turned into patchwork rags, where only a few pieces of semi-natural habitats are left. The use of remaining semi-natural habitats as refuges for many species has frequently been discussed and investigated (Hendrickx et al. 2007, Gaujour et al. 2012, Mitchell et al. 2014). Small distances to semi-natural habitats can increase ecosystem service provision of surrounding agriculturally used habitats (Mitchell et al. 2014) and enhance diversity, whereas the size of these retreats appears to be unimportant (Hendrickx et al. 2007).

Landscapes face homogenization via intensive land use and identical management of large areas, as well as monocultural agriculture. On the global scale this phenomenon is illustrated by a blender which homogenizes communities of animals and plants though anthropogenic influences (Olden 2006). Habitat homogenization (Atauri and Lucio 2001, Gaujour et al. 2012, Tscharntke et al. 2012, Gámez-Virués et al. 2015) and the corresponding loss of microhabitat variety (Anderson 1978) in turn, causes diversity loss. Many different animal groups are limited by 'keystone structures' of the

vegetation, which are defined as important determinants that provide crucial goods and services including shelter and food (Tews et al. 2004). Of course, impoverishment of habitats through land-use change also affects heterogeneity of inhabiting communities. Even slight increases of land-use intensity have detrimental effects on community heterogeneity in above- and belowground communities of both producers and consumers (Gossner et al. 2016).

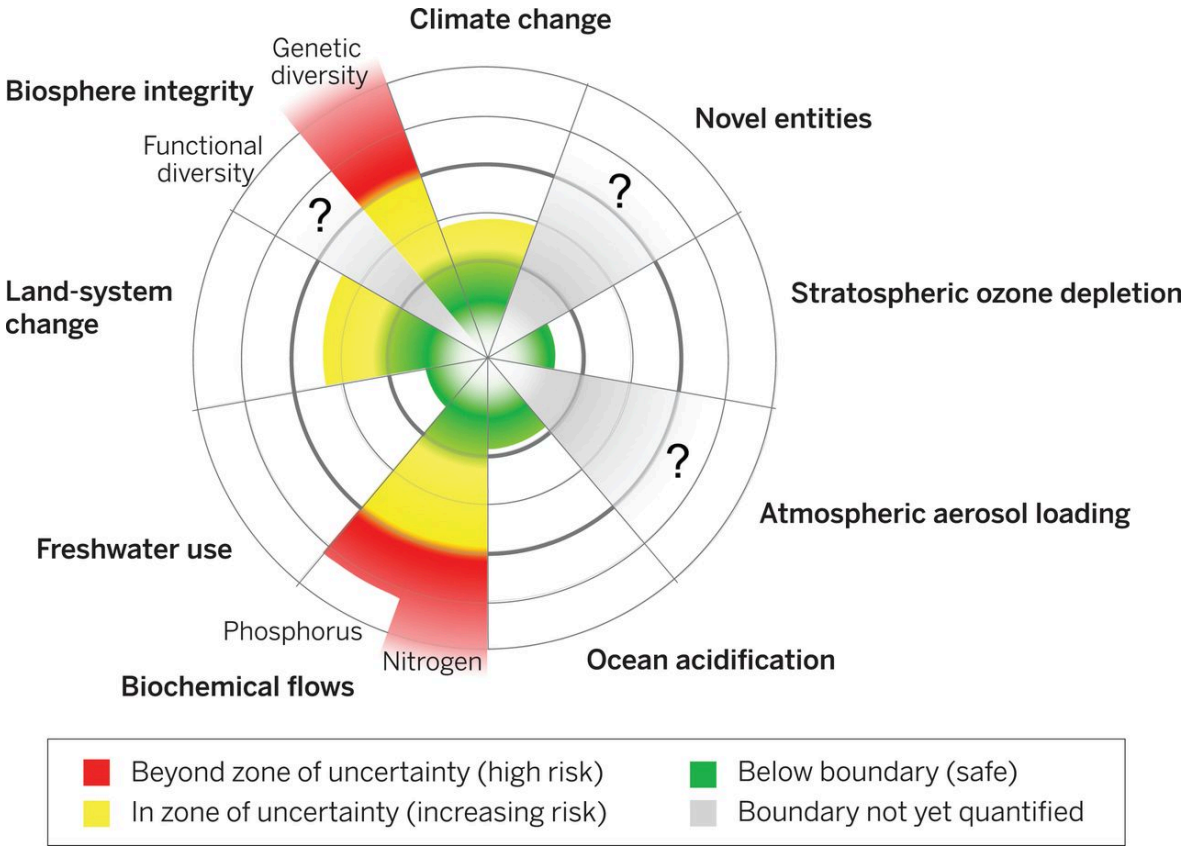

Figure 1.1: Planetary-boundaries system by Steffen et al. (2015). The graphic represents the "current status of the control variables for seven of the planetary boundaries. The green zone is the safe operating space, the yellow represents the zone of uncertainty (increasing risk), and the red is a high-risk zone." (Steffen et al. 2015; 347:1259855-6). 'Biosphere integrity' is a proxy for the two key units of biodiversity (genetic and functional diversity).

Grassland management effects: fertilization, mowing and grazing

In temperate grassland ecosystems land use is mainly represented by fertilization, mowing or grazing. The three management types are not independent from each other. For example, fertilization increases mowing frequency, whereas grazing reduces mowing frequency.

To increase productivity of grassland plants, nutrient application is the first step to gain more biomass. Nitrogen addition rapidly increases total productivity of nitrophilous plants (Garratt et al. 2010, Gaujour et al. 2012, Socher et al. 2012). Nutrient accumulation in global ecosystems not only affects plant growth, but also substance turnover. In addition to the above-mentioned planetary boundary of biodiversity loss, the boundary of N and P flows (e.g. through fertilizer application) has also already been exceeded (Steffen et al. 2015; see Fig. 1.1), although it varies across regions. N and P addition have different adverse effects on ecosystems (Tilman et al. 2001). Both elements drive

eutrophication of soils and surface waters, which in turn can be detrimental for many species that are dependent on certain nutrient levels and cause diversity loss. The effects of N addition have been investigated several times and significant species loss and changes in community composition have been reported (Tilman et al. 2001, Van Den Berg et al. 2011a, Socher et al. 2012, Simons et al. 2014), as well as increases in greenhouse gas emissions (Holland et al. 1999). Nutrient limitation is one of the major factors that drives plant diversity in grassland ecosystems of a Californian nature reserve (Harpole and Tilman 2007). Fertilization causes loss of plant species that are specialized on low-nutrient levels in the soil, and thus causes dominance of a few nitrophilous species that occupy the free niches (Harpole and Tilman 2007).

Not all organisms are negatively affected by nutrient accumulation, as it is reported that some species profit from increased nitrogen availability. Generalized species of sap-sucking insects (Nickel and Hildebrandt 2003) and detritivores (Haddad et al. 2000) benefit from increased nutrient supply, as well as grasses (Garratt et al. 2010, Gaujour et al. 2012), and some herbivorous insects show higher abundances on sites with enhanced nutrient supply (Ritchie 2000, Haddad et al. 2000, Garratt et al. 2010).

Cutting of grasslands primarily prevents scrub encroachment, and thus is essential for grassland ecosystems to exist. Grassland maintenance can appear as mowing or grazing by mammalian herbivores. The intensity and method of maintenance, however, matters for accordance with biodiversity and ecosystem functioning. Sustainable ways of grassland preservation and the balancing act of productivity and sustainability has often been addressed by scientific studies (Gardiner and Hassall 2009, Humbert et al. 2009, Cizek et al. 2012, Müller et al. 2016). Mowing equipment, as well as the date and frequency of cutting is crucial for the preservation of grassland flora and fauna (Humbert et al. 2009, 2010, Cizek et al. 2012, Allan et al. 2014). It has been revealed that leaving uncut patches, or mowing connected meadows on different mowing dates best supports faunal diversity (Humbert et al. 2009, 2010, 2012, Cizek et al. 2012). Floral diversity can also decline with early and frequent mowing, which can be explained by the loss of important reproductive organs and the reduced ability to sprout again (Socher et al. 2012). To save sensitive and less competitive species and thus floral diversity, late mowing dates and a moderate number of cuts are advantageous (Socher et al. 2012). Grassland maintenance by moderate grazing seems to be a suitable way to preserve diverse habitats and ecosystem quality (Bilotta et al. 2007). Besides the effects on grassland architecture caused by grazing animals, the direction of effects on grassland diversity is dependent on livestock species and size (Rook et al. 2004). Bison grazing in north American prairies, for instance, can result in increased grasshopper diversity (Joern 2005). Accurate grassland management by grazing can have positive effects on nutrient cycling, propagule distribution, and on biodiversity through enhancement of vegetation heterogeneity (Rook and Tallowin 2003, Bilotta et al. 2007). Excessive grazing, however, can have opposite effects by degrading soils and surface waters, increasing compaction of soils and decreasing infiltration, and by biodiversity decline (Bilotta et al. 2007).

In summary, it can be stated that the intensity of the single management types is the factor that determines the quality of habitats and biodiversity. Not only the extent, but also the variation in management between the years has been shown to be beneficial for diversity of multiple taxa in central European grasslands (Allan et al. 2014).

Herbivorous insects in grassland ecosystems

Herbivorous insects are a vital part of grassland ecosystems, since these organisms perform the function of biomass conversion and have multiple effects on grassland communities; among others they are an important resource for many predatory organisms. Herbivorous insects have the opportunity to select their food plants through their multiple gustatory receptors on their mouthparts (Chapman 2003) and folivores (leaf chewing) feed on a considerable proportion of grassland vegetation (Köhler et al. 1987, Blumer and Diemer 1996). Through their ingestion, digestion and excretion of plant material, their frass represents an easily transformable substance for soil organisms and plays an important role in nutrient recycling (Samways 1994, Blumer and Diemer 1996, Belovsky and Slade 2000, Bardgett and Wardle 2003). For these reasons, it is likely that herbivores directly influence the diversity and community composition of belowground organisms (Bardgett and Wardle 2003). Likewise, it has been reported that herbivorous insects regulate the composition of plant communities. This is confirmed for folivores (Belovsky and Slade 2000, Joern 2005, Zhang et al. 2011) and expected for sap-sucking herbivores (Nickel 2003). One reason is the increased growth of plant species that are refused by insect herbivores (Zhang et al. 2011). Another possible reason is the increased nutrient availability through herbivory, which favours plant species with adaptations to higher resource availabilities in North American prairies (Belovsky and Slade 2000).

Why are herbivorous insects declining?

A decline of herbivorous insects through land-use intensification can have various causes. Most obviously and often discussed by ecologists may be relevant bottom-up effects, i.e. plant-derived influences on consumers. Herbivorous insects are dependent on resources that are directly influenced by grassland management and their dependency on host plants is shaped by their degree of dietary specialization. Monophagous and oligophagous species occur only when their host plants occur, while polyphagous species can choose between different resources. By now it is unmistaken that decreasing diversity of host plants causes declines in herbivorous-insect diversity (Haddad et al. 2001, Kleijn et al. 2009, Scherber et al. 2010, Simons et al. 2014) and abundance (Scherber et al. 2010). As mentioned above, plant species diversity declines with increased fertilization (Harpole and Tilman 2007, Kleijn et al. 2009, Socher et al. 2012, 2013, Simons et al. 2014, Müller et al. 2016) and mowing intensity (Socher et al. 2012). An increase of total plant biomass, which is promoted by fertilizer application, decreases species richness of herbivores (Joern 2005).

The species richness of the herbivore community is not only impacted by plants as a food resource, but also by their function as shelter and action spaces. The vegetation architecture and structure are

important drivers of biodiversity, since specific small-scale variation can create microhabitats for the requirements of different species (Lawton 1983). Microhabitats can differ in quality in terms of microclimate, which includes temperature, humidity or wind exposure, but also in availability of suitable oviposition sites or shelter from predators (Joern 1982). Those species that are dependent on grass leaves for oviposition are particularly susceptible to mowing practice and will thus decrease in abundance or eventually disappear (Ingrisch and Köhler 1998). Structural complexity is an important driver for the diversity of small grassland insects including herbivores (Dennis et al. 1998).

Mowing has adverse effects in the context of microclimate and shelter, as it causes tough and immediate changes in the sward length. The cutting down of meadows can increase the predation pressure on herbivorous insects, besides the direct killing of them by mowing machines (Humbert et al. 2009, Cizek et al. 2012). Densities of Orthoptera on European hay meadows for instance can be reduced by 65 – 85% (Humbert et al. 2010). This increased mortality in Orthoptera can very likely be transferred to other grassland insect-taxa. Through simultaneous cutting of large areas, possible refuges for the grassland fauna might disappear. The larger the area, the longer is the distance for potential immigrating individuals. Mowing during the warm and dry season leads to unsuitable habitats for herbivores, as shade-giving vegetation is removed and the risk of overheating increases (Gardiner and Hassall 2009).

Furthermore, as confirmed for other taxa (Di Giulio et al. 2001, Simons et al. 2015), herbivorous insects also show the pattern that only a few species have high abundances, large distribution areas and are disturbance-tolerant, whereas the major part of the species pool contains rare and inflexible species (Chisté et al. 2016 and see Chapter II). This might have the same reason as in plants, which display decreased diversity with increased disturbance: a shift in competitive ability to some single species through better adaptation to the current conditions.

Studying communities in real-world ecosystems

The Biodiversity Exploratories is a German-wide multidisciplinary project, which is focussing on functional biodiversity research. As part of the project the influence of anthropogenic land-use on real-world ecosystems has been studied since 2006. The priority of this project is (1) to understand relationships between different taxonomic groups, all facing the same intensity of land use, (2) to understand land-use effects on biodiversity and (3) to study biodiversity effects on ecosystem processes and stability.

Therefore three study regions across Germany have been established, which represent many different possible habitat types. In the northeast the biosphere reserve ‘Schorfheide-Chorin’, in central Germany the national park and surrounding areas of ‘Hainich-Dün’, and in the southwest the biosphere reserve ‘Schwäbische Alb’ act as study areas for a multidisciplinary pool of researchers. In each area 50 forest and 50 grassland sites cover a broad gradient of land-use intensity, which is in grasslands defined by the intensity of fertilization, mowing and grazing. To facilitate the comparison among the sites and standardise for all regions, the land-use-intensity-index LUI has been established

(Blüthgen et al. 2012), which is calculated yearly for each site as,

$$LUI_s = \sqrt{\frac{F_s}{F_r} + \frac{M_s}{M_r} + \frac{G_s}{G_r}}$$

where F is fertilization intensity (kg N • ha^{-1} • year^{-1}), M is mowing intensity (cuts • year^{-1}) and G is grazing intensity (livestock units • grazing days • ha^{-1} • year^{-1}) on site s, standardized by the mean intensity of all regions (r).

Doubtless many studies have investigated the influence of land-use intensity on different organism communities and ecosystems, but not to the extent as this project, which integrates long-term, large-scale and multidisciplinary observations. The study of the above-mentioned effects in real-world ecosystems, rather than experimentally transformed field sites, helps us to understand the real-world consequences of land-use practices.

Aims of the study and research outline

It is of primary importance that we illuminate the complex consequences of human activities. Land use is the major driver of habitat alteration and its impacts on organisms can differ enormously among feeding guilds, trophic levels, taxa or communities. The current thesis aims to contribute to the knowledge of land-use effects on herbivorous insect communities and single species in real-world ecosystems as well as their response in terms of nutrient regulation in lab experiments, addressing the following research objectives:

1) Understanding land-use effects on communities

In chapter I and II, I will disentangle the effects of land use on communities of Orthoptera (grasshoppers and long-horned grasshoppers), plant- and leafhoppers (Auchenorrhyncha). In this context communities were studied as a whole, considering total species richness, abundances, densities or abundance-weighted diversity measures. I will provide insights into the effects of compound land-use intensity (LUI), as well as the single management types of fertilization, mowing and grazing. Orthoptera are leaf-chewing (folivores) and Auchenorrhyncha are sap-sucking herbivores. They share the group of insect-herbivores, but through their different feeding guilds they do not directly compete for resources, which makes it interesting to examine both groups separately.

Additionally, I will present the differences in species richness and species turnover among communities that are known as β-diversity in chapter II. Community heterogeneity can be analyzed in various ways. In the present work two approaches are applied to find potential influences of land-use intensity on β-diversity: first, the differences between community-samples are compared in terms of their species number; second, the differences are compared in terms of community composition. A common way to examine β-diversity is to compare sites on a large scale, e.g. across Germany; chapter II will focus on the small scale by looking at possible homogenization effects

within the sites.

The studies were conducted in the three regions of the Biodiversity Exploratories, and involved seven sampling years of all 150 grassland sites for Orthoptera, and 140 grasslands sites in one year for plant- and leafhoppers.

2) Understanding land-use effects on single species

It is important to understand the impacts of land use on whole communities. In addition to this basis, I will demonstrate in chapter I and II the importance of considering also single species' responses to land use. In most cases where species-responses to environmental gradients are studied, rare species are excluded from analysis (Lord et al. 2015, Foord et al. 2015, Filgueiras et al. 2015). The frequently mentioned reason is the lack of statistical reliability or the inability to show trends through low total abundances and site occurrences. Compositional community-analyses (ordinations) or abundance-weighted diversity measures (Shannon, Simpson diversity) are also not sensitive to rare species responses. However, rare species are important contributors to communities, which are typically composed of a few common and many rare species. For that reason I will present an opportunity to consider also rare species in single-species analyses.

For each of the 29 grassland-Orthoptera species and the 117 plant- and leafhopper species a single 'land-use niche' was calculated which reflects the species' main occurrence along the land-use gradient. The niches were calculated by abundance-weighted means of the land-use intensities of the sites on which the species occurred. A null model subsequently provided an estimated value that can be compared with the observed value. With the help of this comparison, species can be characterized as 'losers' or 'winners' of high land-use intensity.

3) Understanding the individual effects of fertilization on herbivores

The success or susceptibility of single herbivorous species in managed grasslands is partly connected with their nutrient regulation and utilization. As fertilization represents a common method to increase the productive output of grasslands, I will examine the impacts of different fertilization regimes on grasshoppers with laboratory experiments in chapter III. In a choice test, three differently fertilized grasses were presented to different species of nymph and adult grasshoppers in order to find potential resource-preferences.

In the second part of this study I will illustrate nutrient utilization by feeding a group of grasshoppers for a period of eleven days with only one of the four differently fertilized resources. After the trial, possible differences among the treatments concerning their performance and food utilization were examined. These were represented by survival, consumption, approximate digestibility (of plant biomass, N and C), N enrichment, %N and %C (in animal biomass and faeces).

CONTRIBUTIONS TO THE RESEARCH CHAPTERS

Chapter I – Losers, winners and opportunists: how grassland land-use intensity affects orthopteran communities[1]

Melanie N. Chisté, Karsten Mody, Martin M. Gossner, Nadja K. Simons, Günter Köhler, Wolfgang W. Weisser, Nico Blüthgen

Author contributions: MNC, KM, MMG, NKS, WWW and NB conceived and designed the experiments. MNC, NKS and GK performed the experiments and collected the data. MNC and NB performed the statistical analyses. KM provided statistical advice. MNC, KM and NB and wrote the manuscript. MMG, NKS, GK and WWW provided editorial advice.

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Chapter II – Intensive land use drives small-scale homogenization of plant- and leafhopper communities and promotes generalists

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Author contributions: MNC, KM and NB conceived and designed the experiments. MNC, GK and JG performed the experiments and collected the data. MNC analyzed the data. MNC, KM and NB wrote the manuscript. GK and JG provided editorial advice.

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Chapter III – Fertilization-mediated changes in grasshopper dietary preference, performance and food utilization

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Author contributions: MNC, NB and KM conceived and designed the experiments. MNC collected the data. MNC analyzed the data. MNC, NB and KM wrote the manuscript.

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[1] For this thesis chapter I is rewritten in British English

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CHAPTER I – LOSERS, WINNERS AND OPPORTUNISTS: HOW GRASSLAND LAND-USE INTENSITY AFFECTS ORTHOPTERAN COMMUNITIES

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ABSTRACT

Land use and corresponding habitat loss are major drivers of local species extinctions. Orthoptera as important grassland herbivores showed different responses to land-use intensity in different studies, and the susceptibility of this group remains unclear. We sampled annually for seven years 150 temperate grassland sites across three regions in Germany, for which land-use gradients were quantified as mowing, grazing and fertilization intensity. We analysed the effects of land-use intensity on orthopteran diversity and community abundance. To describe species-specific responses to environmental gradients, we employed a new approach termed 'niche model', coupled with a randomization procedure, which is sensitive even for rare species for which trends may otherwise be difficult to detect. Based on abundance-weighted means for each species we quantified the species' occurrence along land-use gradients and identified potential losers and winners of intensive land use.

Overall high land-use intensity negatively affected orthopteran diversity across years and regions, corresponding to decreases with high fertilization, mowing and grazing intensity. Intensive mowing and grazing negatively affected abundance. Diversity and abundance increased with the time after the last cut. The niche model detected 15 out of 29 Orthoptera species as losers of land use, showing significant higher abundance in grasslands with low intensity land use. Two species were winners of high land-use intensity, whereas the remaining 12 were assigned as opportunists. Most species were losers of high fertilization intensity, followed by frequent mowing. Grazing intensity was least detrimental at the species level. Omnivorous, herbivorous and graminivorous species did not differ in their response to land-use intensity, whereas bryovorous/lichenivorous *Tetrix* species showed consistently negative responses to intensive land use.

Our highly replicated, long-term and large-scale survey suggests that further land-use intensification threatens many Orthoptera and causes a consistent diversity loss. Low intensity of fertilization, infrequent mowing and variable grazing will help to maintain a high diversity of orthopterans. The generality of our niche model approach advances studies on species' susceptibility in various study systems.

Keywords: anthropogenic disturbance; Biodiversity Exploratories; effective Shannon diversity; feeding habit; grasshoppers; grassland management; habitat niche; insect herbivory; land use; mowing date; Orthoptera.

INTRODUCTION

The current loss of species is to a great extent caused by anthropogenic influences (Pimm et al. 1995, Hooper et al. 2005), especially by land-use change and intensification (Tilman et al. 2001) and by the corresponding loss or fragmentation of habitats (Krauss et al. 2010). Intensified land use is often described to decrease biodiversity, such as plant species richness (Haddad et al. 2000, Kleijn et

al. 2009) and insect diversity (Haddad et al. 2000, Allan et al. 2014). These negative effects are often related to nitrogen input by fertilization (Van Den Berg et al. 2011a, Socher et al. 2012, Simons et al. 2014). Decreased biodiversity translates into decreased ecosystem performance and stability, which can partly be explained by a loss of functional diversity (Tilman et al. 1997, Birkhofer et al. 2015). Reduced plant species richness for instance has a negative effect on the temporal stability of net productivity (Tilman et al. 2006) and may decrease the resistance of communities against invasive species (Hooper et al. 2005). Many trophic levels in turn suffer from reduced species richness of plants. Microbial biomass and fungal abundance decline with decreasing plant species richness (Zak et al. 2003) and arthropod species richness declines (Haddad et al. 2001, 2009, Allan et al. 2014, Simons et al. 2014), especially of herbivorous insects (Scherber et al. 2010).

Among arthropods, Orthoptera are important herbivores in grassland ecosystems as they consume a considerable portion of grasses and forbs (Köhler et al. 1987, Blumer and Diemer 1996), regulate plant community structure (Zhang et al. 2011) and are important food organisms for birds (Ingrisch and Köhler 1998), spiders and lizards (Ingrisch and Köhler 1998). The functional role of Orthoptera in grassland ecosystems is also illustrated by their influence on nutrient cycling by enhancing the conversion of biomass through their easily transformable frass (Samways 1994). Orthoptera are widespread across grasslands and often sensitive to environmental changes (Guido and Gianelle 2001, Gardiner et al. 2002, Jonas and Joern 2007, Bharamal and Koli 2014), which makes them suitable for studying land-use effects on biodiversity.

Responses of Orthoptera communities to land use and other disturbances have been described by different studies across different ecosystems and showed distinct consequences. Studies in temperate grasslands showed that intensive grazing reduced orthopteran species richness and Shannon diversity (Branson and Sword 2010), fertilization led to reduced survival (Ebeling et al. 2013) or decline in orthopteran species richness (Marini et al. 2008), and mowing strongly reduced grasshopper densities (Humbert et al. 2010). In addition to direct management effects like increased mortality by mowing, indirect effects such as changes in plant community composition can also affect orthopteran communities (Jonas et al. 2002, Schaffers et al. 2008, Unsicker et al. 2010, Hao et al. 2015). However, also positive effects of nitrogen addition on orthopteran densities (Ritchie 2000, Haddad et al. 2000) have been reported. Grazing and mowing showed both positive and negative effects on Orthoptera diversity and abundance (Ingrisch and Köhler 1998), depending on management intensity. Data from extensive long-term studies with consideration of the susceptibility of all local Orthoptera species – abundant species as well as rare species – is needed to better understand the variation in susceptibility of this important group of herbivores.

We studied responses of Orthoptera to grassland land-use within a large-scale and long-term project in three regions of Germany (Fischer et al. 2010). These grasslands are managed by fertilization, mowing and grazing with different intensities (Blüthgen et al. 2012). By covering a broad range of land-use intensities, this research platform provides unique opportunities to study determinants of

orthopteran community structure in an authentic scenario, which is an alternative to laboratory and artificial field studies.

Here we examined the effects of land-use intensity on orthopteran abundance, diversity and community composition, particularly the influence of the different management types: fertilization, mowing, and grazing. To infer causal effects of the three management types on orthopteran communities, we compared Orthoptera diversity and abundance with their incidence. In extension to other studies on Orthoptera responses to land use, we investigated these responses on a species-specific level and analysed the niche breadth of single species with a niche model combined with a randomization approach. For each Orthoptera species, we defined a 'habitat niche' based on the occurrence and abundance across 150 grassland sites of variable land-use intensities during seven years, allowing us to distinguish losers, winners and opportunists of intensified land use. In contrast to aggregate diversity measures like the common Shannon diversity, species richness or other multispecies indices (Vačkář et al. 2012), this methodology considers rare species and gives an opportunity to evaluate each species' response along environmental gradients. Our simple approach can also be used to describe the species' responses to other environmental gradients e.g. temperature, pH or moisture.

Based on findings from other studies (Hohl et al. 2005, Marini et al. 2008, Branson and Sword 2010, Humbert et al. 2010), we expected intensive land use to decrease orthopteran abundance and diversity, leading to more species being losers than winners within the community, that is, more species predominantly occur at low-intensity grasslands.

MATERIALS & METHODS

Study Site

The study was conducted within the framework of the Biodiversity Exploratories, which covers three different regions across Germany (Fischer et al. 2010), the biosphere reserve Schorfheide-Chorin (SCH; 53°02'N 13°83'E, 2–139 m a.s.l., area about 1300 km^2, annual mean precipitation 500–600 mm, mean annual temperature 8–8.5 °C) in the northeast, the national park of Hainch-Dün and its surrounding areas (HAI; 51°20'N 10°41'E, 285–550 m a.s.l., 1300 km^2, 500–800 mm, 6.5–8 °C) in the centre and the biosphere reserve Schwäbische Alb (ALB; 48°43'N 9°37'E, 460–860 m a.s.l., 420 km^2, 700–1000 mm, 6–7 °C) in the southwest of Germany. Every area contains 50 grassland sites (each 50 m × 50 m), which represent agriculturally used meadows or pastures along a land-use intensity gradient and are managed by local farmers. Type and intensity of management is assessed yearly since 2006 by standardized interviews with the farmers and landowners. The three components that shape land-use intensity of grasslands – fertilization (kg N • ha^{-1} • $year^{-1}$), mowing (cuts $year^{-1}$) and grazing (livestock units • grazing days • ha^{-1} • $year^{-1}$) - are combined in an index of land-use intensity (LUI, (Blüthgen et al. 2012). The LUI was calculated as the sum of the globally standardized

land-use components (intensities per site were divided by the global mean of all sites in all regions) of each site and then square root transformed for a more even distribution.

Sampling design

The study was conducted from 2008 to 2014, assessing orthopterans in 150 grassland sites of the three regions. In 36 out of 1050 sampling occasions, sites could not be sampled in a given year because entering was not permitted at the survey time. Sampling from 2008 to 2013 was conducted twice per year in June and August, where each site was sampled by standardized sweep-netting during a long-term arthropod survey (Simons et al. 2015). On each grassland site, 60 double sweeps were conducted along the borders of the site, which are 200 m in length. For the analyses we only included sites which were sampled twice per year. In 2014 we conducted a more specific sampling campaign for orthopterans with a biocenometer (1 m × 1 m area, height 0.6 m), which is an aluminium frame covered with gauze and is quickly placed on an area to prevent insects from fleeing the area before capture. This method provides an assessment of standardized densities of both active and inactive individuals and a more complete sampling by covering the herb as well as the ground layer. In August 2014 each region was sampled within 14 days, by randomly sampling ten units of 1 m^2 on each site along the same transect as above. All Orthoptera were collected and determined to species level (determination 2014: M. N. Chisté, 2008 – 2013: G. Köhler). Our analyses are based on a total of 3752 adult individuals (2099 in 2014 with the biocoenometer; 1653 by sweep-netting in 2008 – 2013) we found from 2008 – 2014.

Data analysis

Combined land-use intensity (LUI) effects on diversity and abundance

Orthopteran diversity was analysed as a response to gradually increasing land-use intensity. To quantify diversity Shannon's diversity index *H*' was calculated for each site and year, which considers both species richness and the abundance distribution. For analysis and graphics the more tangible effective Shannon diversity $e^{H'}$ (Jost 2006) was used, which can be interpreted as 'effective' number of species and is more intuitive than the Shannon's index of uncertainty *H*'. As $e^{H'}$ is not zero, but one, if only one species occurs on a site, the differentiation between sites with only one species ($e^{H'} = 1$) and empty sites ($e^{H'}$ defined as 0) was possible. Abundance obtained for the sampling year 2014 refers to the total number of adult Orthoptera in 10 m^2; in 2008 – 2013 it refers to the sum of Orthoptera adults sampled by 120 double sweeps during the two sampling dates. Data analyses were performed with the statistical software R 3.1.2 (R Core Team 2014). The across-years analysis was conducted using linear mixed effects modelling with 'lmer' within the package 'lme4' (Bates et al. 2015). The response of orthopteran $e^{H'}$, abundance and species richness was analysed to the fixed explanatory variables LUI and region, and the interaction of both. LUI was calculated independently for every study year, as land-use intensity on each site can change annually. LUI of the previous year was considered to account for possible long-term effects of land use, but no considerable difference between the fits of

the models with both LUIs (see supplementary material Table S1) was found. Year and siteID were defined as random factors with own random intercepts to standardize for overall interannual variation and to consider repeated measures of the same sites. For diversity as response variable, for example, the syntax of our model was defined as diversity ~ region * land-use intensity + (1|year)+ (1|siteID). For within-years analyses, linear modelling was used within the package 'nlme' (Pinheiro et al. 2014), testing the effects of LUI, region and their interaction on $e^{H'}$. The syntax in R was the same as above without random effects.

In earlier analyses we tested the effect of the size of the whole grassland, containing our 50 x 50 m sites, which is managed in the same way as the respective site, and found no effect of this factor on all response variables. This factor is therefore not included in our model.

Effects of fertilization, mowing and grazing on diversity and abundance

To assess the influence of the individual management types, fertilization, mowing and grazing, our response variables were related to these factors as described above for the effects of LUI. Our response variables were then compared with the incidence of each of the three management types, i.e. fertilized/unfertilized, mown/unmown and grazed/ungrazed. In addition to the effects on all sites, we analysed the effects of mowing, grazing and fertilization intensity with exclusion of unmown, ungrazed and unfertilized sites. Modelling occurred as described above. For the temporal effects of mowing, our response variables were related, exemplarily for 2014, to the number of days between the last cut and the sampling date by linear modelling for the sites, where this information was available.

Abundance-weighted means and niche model

To define the ecological niches of orthopterans on a species level, abundance-weighted means (AWMs) of land-use intensity for each species were calculated. AWMs of the LUI, fertilization, mowing and grazing intensity were calculated. AWM_i of a species i was calculated as

$$AWM_i = \sum_{s=1}^{150} \sum_{y=2008}^{2014} p_{i,s,y} \cdot L_{s,y}$$

where $p_{i,s,y}$ is the proportion of individuals of species i found in site s in year y in relation to its total abundance across all sites and all years ($\Sigma_s \Sigma_y p_{i,s,y} = 1$) and $L_{s,y}$ is the land-use intensity on site s in year y. $L_{s,y}$ was calculated for each year using respective land-use intensities of the sampling year. We also checked the analyses with previous years' LUI and found that AWMs of previous years strongly correlated with AWMs of respective years. As a proxy for the niche breadth of a species, we also calculated the abundance-weighted standard deviation AWSD, weighted by the proportion of abundance.

For statistical analysis of the AWMs we have chosen a randomization approach, based on the null model that an Orthoptera species can occur on every site with the same likelihood and describes the most probable site conditions for that species. The null model chooses LUI, mowing, grazing or

fertilization intensities of random sites for each species, considering the number of sites, where this species occurs and calculates after 10,000 iterations an expected value of the site conditions for each species. To avoid repeated consideration of sites, intensities were averaged across the years 2008 – 2014 for the null model. The null model was restricted to the one, two or three regions in which the species was recorded (Table S2), e.g. when a species only occurred in region ALB, the null model picked a given number of sites from the pool of 50 sites in ALB only. The objective of this restriction was to consider distribution boundaries of single species across Germany. As in any randomization model, the proportion of AWMs from 10,000 null models with greater or smaller AWMs respectively than the observed value provides the p-value for the significance of the deviation between observed and expected values. Species with significantly smaller observed than expected AWMs were declared as 'losers', species with significantly higher AWMs than expected were declared as 'winners'. For species which could neither be classified as 'losers' nor as 'winners', we tested whether they could be specialized on intermediate land-use levels, i.e. whether they have an intermediate AWM with a narrower niche than expected. Therefore, we compared the observed and expected weighted coefficient of variation (CV = AWSD/AWM) to account for the increase in standard deviation with increasing mean. This comparison allows us to distinguish 'opportunists' (observed CV ≥ expected CV) from species that are 'specialized' on intermediate land-use intensities (observed CV < expected CV and species not only occurred on one site, i.e. CV ≠ 0); the latter apply only to those species that are not significant winners or losers.

The different feeding habits of each species (Ingrisch and Köhler 1998) were classified, which are herbivorous (H) feeding on different plants, graminivorous (G) feeding on grass only, omnivorous (O) feeding on animals and plants and bryovorous-herbivorous (BH) species feeding on moss, algae, lichens and plants and tested if AWMs responded differently to the feeding habits based on an ANOVA.

Leptophyes punctatissima (Bosc, 1792)*, Meconema thalassinum* (De Geer, 1773) and *Tettigonia viridissima* (Linnaeus, 1758) were excluded from the niche analysis, because these species are shrub or tree-dwelling and occur only coincidently in grasslands (Ingrisch and Köhler 1998).

RESULTS

Combined land-use intensity (LUI) effects on diversity and abundance

A total of 32 Orthoptera species out of eight subfamilies were recorded in 150 sites, thereof 19 in ALB, 19 in SCH and 14 in HAI. The mean (± SE) orthopteran effective Shannon diversity $e^{H'}$ of 2008 – 2014 (Fig. 2.1a) was highest in region SCH (1.51 ± 0.05), followed by HAI (0.87 ± 0.05) and ALB (0.82 ± 0.06). Mean abundance per site (Fig. 2.1c) was highest in region SCH (5.72 ± 0.66), followed by ALB (2.90 ± 0.31) and HAI (2.88 ± 0.34). Both diversity and abundance differed significantly across regions in 2014, but not based on the earlier data set (Table S 2.3).

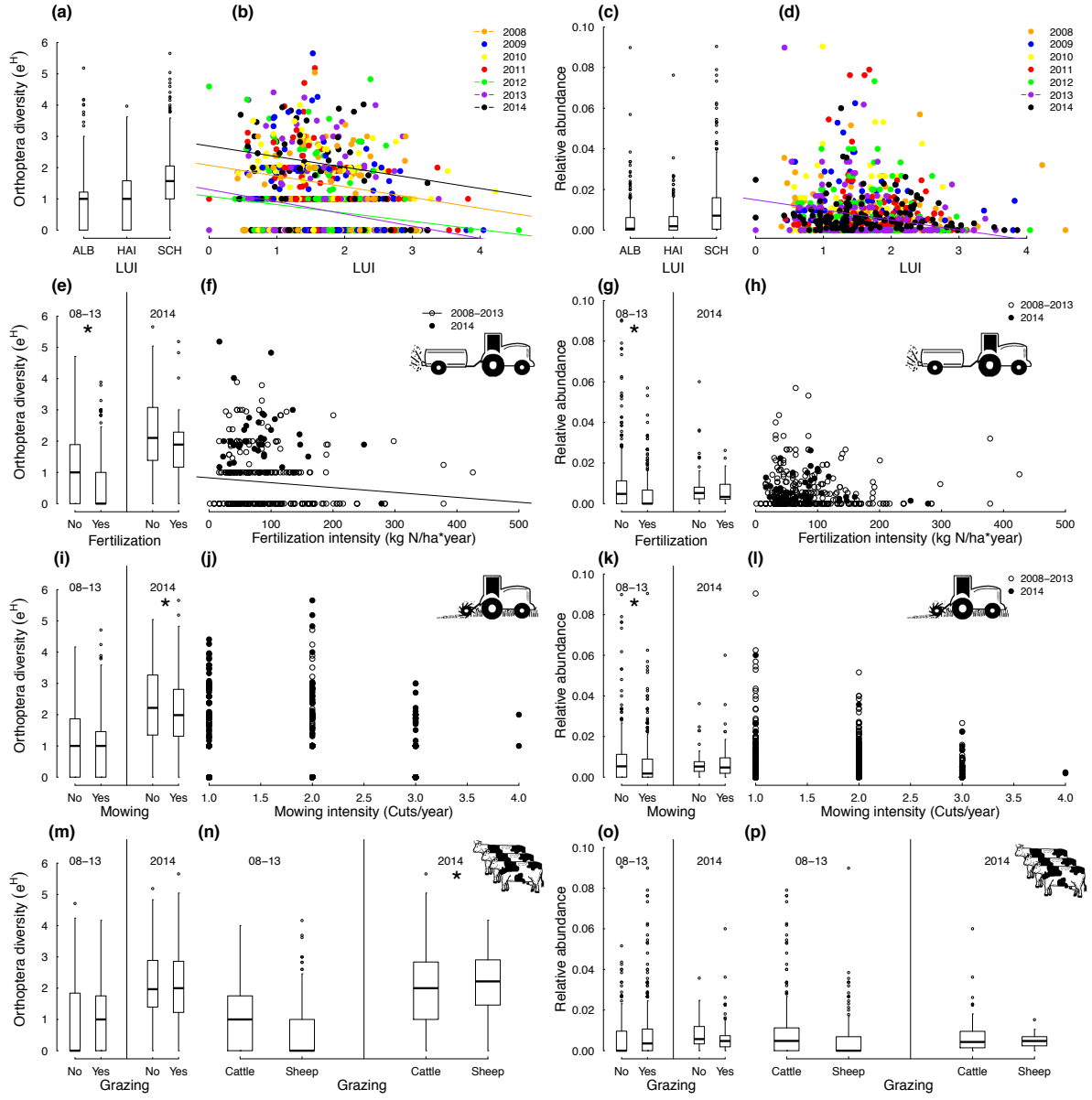

Figure 2.1: Differences in orthopteran effective Shannon diversity $e^{H'}$ (a) and relative abundance (c) between the three regions ALB, HAI and SCH in all study years and response of $e^{H'}$/abundance to combined land-use intensity LUI (b/d) on fertilized vs. unfertilized sites (e/g), to fertilization intensity [kg N • ha^{-1} • year^{-1}] within fertilized sites (f/h), mown vs. unmown sites (i/k), mowing intensity [cuts/year] within mown sites (j/l), grazed vs. ungrazed sites (m/o), and cattle-grazed vs. sheep-grazed sites within grazed sites (n/p). Relative abundance refers to total abundance in each study year.

Orthopteran diversity, but not abundance, declined significantly with increasing land-use intensity, consistently across all regions and years, both in 2008 – 2013 ($F_{1,424.4} = 10.42$, $P < 0.01$) and in 2014 ($F_{1,134} = 13.21$, $P < 0.001$, further information in Table S 2.3).

When analysing years separately, in four out of seven years increasing LUI significantly reduced orthopteran diversity (Fig. 2.1b), in the remaining three years no significant effects despite a consistent trend (Table S 2.4) was found. LUI significantly decreased Orthoptera abundance in 2013, but not in the remaining years (Fig. 2.1d, Table S 2.4). Predominant negative slopes also confirmed negative effects on orthopteran diversity and abundance, even in years or regions, where effects were not significant (Table S 2.4). Results for species richness were consistent with results for $e^{H'}$ (Table S 2.3).

Table 2.1: Management effects on Orthoptera diversity and abundance. We distinguish between effects of intensity (Int) of fertilization [kg N • ha^{-1} • year^{-1}], mowing [cuts/year] and grazing [livestock units • grazing days • ha^{-1} • year^{-1}], of the sampling region and of the interaction between region and intensity on orthopteran effective Shannon diversity $e^{H'}$ and abundance in all three regions during the two sampling periods. Significant effects of management intensity are shown in bold.

		2008-2013			2014		
		All regions			All regions		
Response		**Int**	**Region**	**Int x Region**	**Int**	**Region**	**Int x Region**
				Fertilization			
Diversity	**Slope**	-0.002			-0.006		
	F	8.619	19.472	0.115	2.076	14.708	2.532
	P	**0.003**	<0.001	0.892	0.152	<0.001	0.083
Abundance	**Slope**	-0.004			-0.039		
	F	0.428	7.447	1.243	<.001	9.209	0.243
	P	0.513	0.001	0.289	0.993	<0.001	0.785
				Mowing			
Diversity	**Slope**	-0.075			-0.282		
	F	1.578	8.362	2.328	4.988	15.137	3.134
	P	0.210	<0.001	0.099	**0.027**	<0.001	**0.047**
Abundance	**Slope**	-0.398			-0.780		
	F	4.694	6.183	0.413	0.112	9.227	0.739
	P	**0.031**	0.002	0.662	0.739	<0.001	0.726
				Grazing			
Diversity	**Slope**	<.0001			-0.001		
	F	0.564	18.368	0.273	5.520	14.647	0.514
	P	0.453	<0.001	0.761	**0.020**	<0.001	0.600
Abundance	**Slope**	0.001			-0.011		
	F	0.023	6.101	0.432	4.909	9.617	0.770
	P	0.880	0.003	0.649	**0.028**	<0.001	0.465

Effects of fertilization, mowing and grazing on diversity and abundance

Fertilization intensity had a significant negative effect on $e^{H'}$ in 2008 – 2013 in all regions, but not in 2014 (Table 2.1). Abundance in all years and all regions was not significantly affected by fertilization intensity. Mowing frequency had a significant negative effect on Orthoptera abundance in 2008 – 2013, but not in 2014 (Table 2.1). Diversity $e^{H'}$ significantly decreased with mowing frequency in 2014, but not in 2008 – 2013. For 2014 we found a significant interaction between region and mowing intensity for diversity. Mowing-intensity effects on $e^{H'}$ were negative in region ALB ($F_{1,46}$ = 13.37, P < 0.01) and HAI ($F_{1,48}$ = 0.001, P = 0.982) and positive but not significant in region SCH ($F_{1,40}$ = 0.07, P = 0.796). Grazing intensity significantly reduced $e^{H'}$ and orthopteran abundance in 2014, while in the remaining years grazing had no significant effects. Orthoptera abundance and $e^{H'}$ differed significantly across regions for the three different management types (Table 2.1). Results for species richness were consistent with results for $e^{H'}$, except that mowing intensity in 2014 had a significant effect on species richness in all three regions (Table S 2.5).

Analysing the incidence of land use (Figs. 2.1e-p, Tables S 2.6, S 2.7), we found that fertilized sites were significantly less diverse than unfertilized sites across the first six sampling years (Fig. 2.1e; $F_{NumDF = 1\ DenDF = 368.35}$ = 5.518, P = 0.019). Within fertilized sites orthopteran diversity significantly decreased with increasing nitrogen amounts applied in 2008 to 2013 ($F_{1,307.04}$ = 5.637, P = 0.018), but not in 2014 (Fig. 2.1f, $F_{1,140}$ = 0.912, P = 0.345). Mown sites had a smaller diversity (Fig. 2.1i;

$F_{1,140}$ = 6.941, P = 0.009) and species richness than unmown sites in 2014 and showed lower abundances of orthopterans in 2008 – 2013 (Fig. 2.1k, Tables S 2.6, S 2.7, $F_{1,266.59}$ = 4.323, P = 0.039). Grazed and ungrazed sites did not differ in diversity (Fig. 2.1m; 2014: $F_{1,140}$ = 0.865, P = 0.174; 2008 – 2013: $F_{1,348.07}$ = 0.771, P = 0.380) or abundance (Fig. 2.1o; 2014: $F_{1,140}$ = 1.358, P = 0.246 ; 2008 – 2013: $F_{1,334.57}$ = 1.288, P = 0.257) in all sampling years. In 2014 cattle-grazed sites were significantly less diverse (Fig. 2.1n; $F_{1,95}$ = 9.704, P = 0.002) and species rich (Table S 2.7) than sheep-grazed sites, and within sheep-grazed sites diversity of Orthoptera also declined significantly with the intensity of grazing ($F_{1,38}$ = 4.49, P = 0.041). Abundance did not differ between sheep-grazed and cattle-grazed sites (Fig. 2.1p; 2014: $F_{1,95}$ = 0.031, P = 0.862; 2008 – 2013: $F_{1,107.55}$ = 0.078, P = 0.748).

Concerning the timing of mowing in 2014, diversity ($F_{1,60}$ = 4.50, P < 0.05) and abundance ($F_{1,60}$ = 4.25, P < 0.05) of Orthoptera significantly increased with the time span since the last cut (Fig 2.2 a, b).

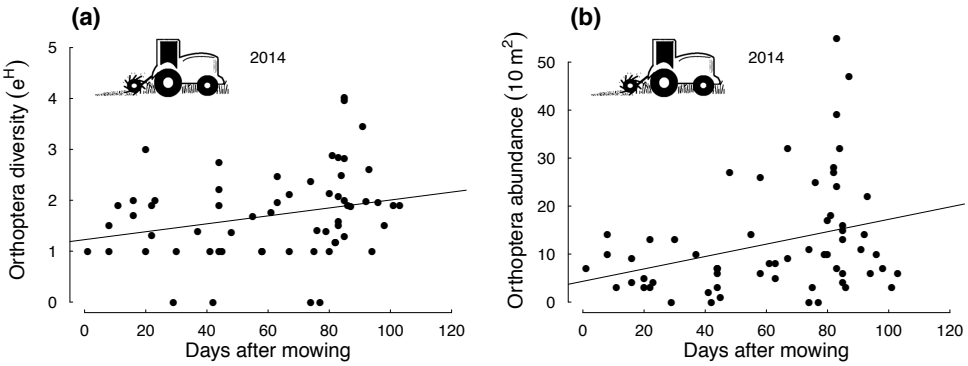

Figure 2.2: Changes in orthopteran $e^{H'}$ (a) and total abundance in 10 m^2 (b) with number of days between mowing and sampling in 2014. All regions (ALB, HAI and SCH) were pooled.

Abundance-weighted means

Most species were found on sites with land-use intensities lower than the mean intensities over all years across all regions. This is illustrated by their AWM on the left side of the dashed line in Figure 2.3. Only few species were winners of high land-use intensity or of high intensities in the three management types (Fig. 2.3, Table 2.2, more detailed in supplementary material, Table S 2.8).

The vast majority of Orthoptera species occurred at higher abundance on sites with low land-use intensity, i.e. their observed abundance-weighted mean (AWM) of LUI was lower than the expected mean LUI based on a random selection of sites (Fig. 2.3a, Table 2.2). One half of our Orthoptera species showed a significant deviation from the null model (losers) and about 40% of species showed no higher abundances on specific LUI (opportunists).

More than 90% had an AWM of fertilization less than expected by the null model, thereof almost a third of the sampled species occurred only on unfertilized sites. Almost a third of our sampled species significantly occurred on less intensively fertilized sites (losers), the rest of the species were opportunists. There was no winner of fertilization intensity (Fig. 2.3b, Table 2.2).

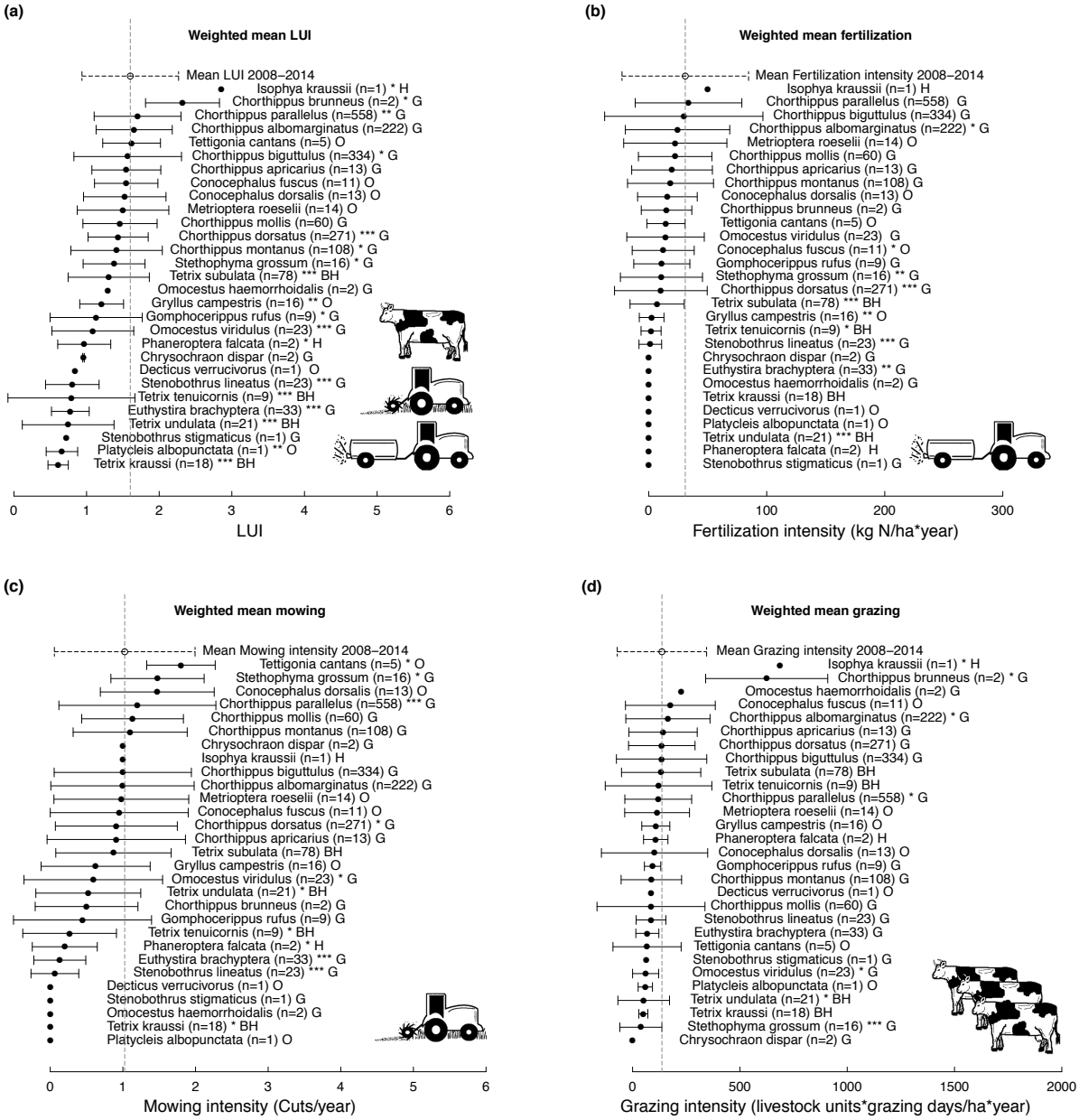

Figure 2.3: Land-use niches of each orthopteran species, reflecting those grasslands in which they occur most frequently: (a) abundance-weighted mean of the compound land-use intensity (LUI) of their sites, (b) the fertilization intensity [kg N • ha^{-1} • $year^{-1}$], (c) mowing intensity [cuts/year] and (d) grazing intensity [livestock units • grazing days • ha^{-1} • $year^{-1}$] from 2008 to 2014, along with weighted standard deviations (corresponding to niche breadth). Open dots in the top represent the mean and standard deviation of land use levels across all 150 sites from 2008 to 2014; abundance is shown in parentheses behind species names. Feeding habits of the different species are herbivorous (H), omnivorous (O), graminivorous (G) and bryovorous-herbivorous (BH).

Most orthopterans occurred on rarely mown sites, more than a quarter had significantly smaller observed than expected AWMs of mowing (losers) and more than 60% were opportunistic concerning mowing intensity (Fig. 2.3c, Table 2.2). Most orthopteran AWMs for grazing intensity were smaller than the expected mean value (Fig. 2.3d, Table 2.2) with almost the same number of species significantly occurring either on strongly grazed sites or on weakly grazed sites, which means that the number of winners and losers of grazing intensity was similar. More than 70% of opportunistic orthopterans concerning grazing intensity were found.

Table 2.3: Orthoptera species that are losers or winners of land-use intensity according to their abundance-weighted mean occurrence. Number and percentage of the 29 Orthoptera species that occurred with significant higher abundances on lower land-use intensity than expected (obs < exp) are shown in bold and declared as 'losers'. Species with 'obs = 0' were only found on sites with intensities of zero (none of the sites had a LUI of zero) and are included in species percentages with bold 'obs < exp'. Species that occurred with significant higher abundances on higher land-use intensities than expected (obs > exp) are shown in bold and declared as 'winners'. 'Opportunists' are species with no significant higher abundance on specific land-use intensities; direction of their occurrences are shown as 'obs < exp' or 'obs > exp'. We show losers, winners and opportunists of the compound land-use intensity index (LUI), fertilization intensity [kg N • ha^{-1} • $year^{-1}$], mowing [cuts/year] and grazing [livestock units • grazing days • ha^{-1} • $year^{-1}$].

	Losers		Winners	Opportunists	
	obs = 0	**obs < exp (p<.05)**	**obs > exp (p<.05)**	**obs < exp**	**obs > exp**
LUI	-	**15 (51.3%)**	**2 (6.9%)**	9 (31%)	3 (10.3%)
Fertilization	9 (31%)	**11 (37.9%)**	**0**	16 (55.2%)	2 (6.9%)
Mowing	5 (17.2%)	**7 (24.1%)**	**3 (10.3%)**	16 (55.2%)	3 (10.3%)
Grazing	1 (3.4%)	**4 (13.8%)**	**3 (10.3%)**	18 (62.1%)	4 (13.8%)

Omnivores, herbivores and graminivores did not differ in their sensitivity to compound LUI (Fig. 2.3) and were found throughout the different land-use intensities. Bryovorous species (*Tetrix* spec.), however, were found predominantly on low intensity sites (Fig. 2.3) and differed significantly from herbivorous species concerning their AWM for the compound LUI (Tukey-Test, $P < 0.01$). Herbivorous Orthoptera differed significantly from bryovorous ($P < 0.01$), graminivorous (Tukey-Test, $P < 0.01$) and omnivorous species ($P < 0.001$) concerning their AWM for grazing intensity.

DISCUSSION

Orthoptera diversity generally decreased with increasing grassland land-use intensity. Among the three management types, fertilization had the strongest negative effect, followed by mowing and grazing. Total Orthoptera abundance did not show a consistent decline, but revealed strong effects at the species level: Most orthopterans had higher abundances at low-intensity grasslands, particularly at unfertilized and infrequently mown sites. This species-level pattern, revealed by a newly developed method, that describes the species' tolerance by combining weighted means with a null model approach, corresponds to diversity decline, but also allows for a more informative and powerful analysis than the analysis of diversity and total abundance alone. Orthopterans seem to be more affected by combined land-use intensity, as we found higher proportions of opportunists within the single management types.

General effects of land use (LUI)

Grasslands with increasing combined land-use intensity (LUI) hosted less diverse orthopteran communities and were often also less frequented by Orthoptera. Also at the species level we found that most of the species were losers of high LUI, some were opportunists and only three species were winners of combined LUI. The combination of the three management types adds up to a stronger disadvantage to grasshoppers than each of them alone. Diversity declines of different insect taxa through intensified land use are known from previous studies (Haddad et al. 2000, Allan et al. 2014,

Simons et al. 2014), where frequent disturbance and habitat loss may be the major reasons for declining diversity. Orthoptera may be susceptible to fluctuations in the appearance of their habitats in intensively managed grasslands, like changes in vegetation height (Gardiner et al. 2002), which alter the microhabitats they need. Different management types will result in different microhabitats and changes, which are discussed below.

The regional differences in orthopteran diversity and abundance are mainly based on the geographical and thus climatic and ecological differences of the three regions and did not occur unexpectedly. Communities differ regionally and species have different altitudinal and habitat distribution boundaries across Germany (Ingrisch and Köhler 1998).

Fertilization

Fertilization was the most influential land-use type in grasslands, showing the strongest negative effects on diversity and single species occurrences with many species not tolerating fertilization at all. Although fertilization increases plant productivity (Ritchie 2000), it often reduces plant species diversity (Bakelaar and Odum 1978, Haddad et al. 2000). Insect species diversity (Haddad et al. 2000), especially of herbivorous insects including orthopterans (Scherber et al. 2010), is positively related to plant species richness in experimental grassland systems, and naturally assembled grasslands (Simons et al. 2014). Plant species richness may also have positive effects on the fitness of grasshoppers (Unsicker et al. 2010). Indeed, in the sampled grasslands researchers also found a strong decrease in plant diversity with increasing land-use intensity (Socher et al. 2013, Simons et al. 2014), corresponding to the decline in Orthoptera species diversity. Simons and colleagues (2014) also concluded that herbivore diversity (including Orthoptera) is more strongly affected by changes in plant diversity than by changes in plant biomass. Fertilization had the most consistent negative effect on plant diversity and positive effect on plant biomass across two years and the three regions (Simons et al. 2014). The increase in plant biomass did however not increase herbivore biomass which could have in turn increased herbivore diversity. Diversity of plants seems thus to play a key role in the context of diversity loss of Orthoptera.

Both plants and herbivores usually benefit physiologically from higher nutrient availability and thus fertilization (Ritchie 2000), but species may suffer from an increased interspecific competition – one important reason why diversity declines whereas abundance remains unchanged or even increases. In fact, higher fertilization intensity led to steeper abundance decay of the whole insect community, including Orthoptera, in the same grasslands through an increased dominance of the most abundant species (Simons et al. 2015). Hence the fertilization-tolerant and most abundant species *Chorthippus parallelus* (Zetterstedt, 1821) may either outcompete fertilization-intolerant species or at least compensate for their absence and thereby stabilizes orthopteran abundance levels. Higher nutrient levels in plant tissues can be beneficial to plant-feeding Orthoptera (Haddad et al. 2000) and can increase performance and reproductive success of the grasshopper *C. parallelus* (Ebeling et al. 2013),

consistent with our finding that this species predominantly occurred on intensively used and fertilized areas. *C. parallelus* seems to be an appropriate indicator for intensive management.

Tetrix kraussi (Saulcy, 1888) was one of the most susceptible species of this study and is known to prefer calcareous habitats with a dry microclimate; listed as threatened in the Red List for Germany. Also the remaining Tetrigidae (*Tetrix* spec.) preferably colonize less intensively managed habitats and thus turn out to be probably useful indicators for extensive grassland management. With fertilization enhancing the productivity of grasslands, open soil spaces disappear (Hochkirch et al. 1999), which are important habitat parameters for Tetrigidae.

An essential reason for the negative effect of fertilization may be a higher vegetation structure and density of grassland plants, because many grasshopper species prefer open grasslands with exposed soil, probably due to climatic conditions and microhabitat preferences for egg-laying (Ingrisch and Köhler 1998).

Mowing

Negative effects of mowing on Orthoptera, as in this study, have often been described, with the killing of individuals through the physical intervention (Humbert et al. 2010), destruction of vital food resources, increased predation pressure (Cizek et al. 2012) and disturbance of a suitable microclimate (Ingrisch and Köhler 1998, Gardiner and Hassall 2009), listed as major reasons. Migration of disturbed populations to intact habitats can also play a role for population decline of several species (Guido and Gianelle 2001). Mowing can reduce orthopteran densities by 65–85%, depending on the properties of the mower such as cutting height (Humbert et al. 2010). The significant reduction of abundance of several Orthoptera species on frequently mown meadows in our study is consistent with current knowledge and corroborates findings of other studies (Humbert et al. 2009). We have looked into the dynamics of diversity changes following mowing: orthopteran diversity and total abundance increased with the time span between sampling and last cut, which may probably be due to more time for migration from neighbouring habitats, re-population and egg hatching.

Species like *Euthystira brachyptera* (Ocskay, 1826)*, Phaneroptera falcata* (Poda, 1761)*, Platycleis albopunctata* (Goeze, 1778) or *Leptophyes punctatissima* (Bosc, 1792) lay their eggs in plants and not into soil and were particularly threatened by mowing, which was also encouraged by Ingrisch & Köhler (1998), who stated reduced ecological resistance to environmental changes for orthopterans with plant-derived egg-laying substrates.

Grazing

Grazing intensity resulted in decreases of orthopteran diversity and abundance, but appeared to be the least disturbing management type, as the proportion of species that were significantly reduced on heavily grazed sites was lower than for fertilization and mowing. Studies have already shown that grazing affects grasshopper community composition (Jonas and Joern 2007) and decreases their

abundance (Simons et al. 2015). Reported effects of grazing on diversity were ambiguous, ranging from positive (Joern 2005) to negative (Branson and Sword 2010) when contrasting grazed and ungrazed sites. In fact we found that as many species benefitted as suffered from grazing. We found no differences between grazed and ungrazed sites, but between sheep-grazed and cattle-grazed sites. Grazing intensity and species identity of grazing animals, their selectivity and body size are major factors that may influence the direction of grazing effects (Rook et al. 2004). Grazing represents a more patchy and gentle way of mowing, because grazing animals are slower, more selective and occur relatively patchy on a pasture, which is likely to facilitate avoidance by mobile grasshoppers. Grazing is also linked to nutrient recycling and high nitrogen availability through animal faeces (Bilotta et al. 2007), which may have parallels to the impact of fertilization on insect communities although it is often spatially more heterogeneous. Grazing or mowing has another positive effect, as it prevents the grasshoppers' habitat from unfavourably high and dense vegetation or even disappearance by long-term scrub encroachment in otherwise untreated grasslands. The advantages of grazing are probable reasons that species, which lay their eggs into plant parts, are less disturbed by grazing than by mowing. The date of mowing or grazing plays an important role, as an early date might erase a majority of present less mobile nymphs, whereas a midsummer date may potentially disturb reproducing adults.

Feeding habits

The consideration of the feeding habits in this study did not show a disadvantage of higher trophic levels with increasing land-use intensity, as it is predicted in other studies (Haddad et al. 2011, Herbst et al. 2013). Specialized grass feeders as much as polyphagous Orthoptera occurred on differently managed sites. The only pattern we could find was that species that feed on moss, algae and plants (Tetrigidae) were more often found on low intensity sites. Bryophytes are known to decrease with strong fertilization, frequent mowing (Müller et al. 2012) and high plant productivity in grasslands (Müller et al. 2014), which increases with land-use intensity (Haddad et al. 2000). Bryophyte species richness is highest on sites with bare ground (Müller et al. 2012), which is also favorably frequented by Tetrigidae.

We found that herbivorous Orthoptera (not graminivorous) differed in their weighted means from all the other feeding guilds, which must be treated with caution, because we only found three individuals out of two species of this feeding guild.

Management implications

The diversity of grassland arthropods like Orthoptera can be supported by a patchy application of mowing (Cizek et al. 2012), or by leaving uncut patches on meadows as refuges (Humbert et al. 2009, 2010), which has the same effect. The selection of equipment together with the mowing date also strongly influences the number of depleted grassland fauna (Humbert et al. 2009, 2010). Later mowing dates in autumn are better than in the phenological peak of orthopterans. There is no perfect mowing

time for all grassland organisms, however, and it seems likely that a yearly rotating mowing date would be best for biodiversity, corresponding to a positive effect of inter-annual variability in land use found for multidiversity (Allan et al. 2014). Annual variation in land-use intensity on the sites may enable the reproduction of species with different phenologies and thus increases diversity. As grazing had the least effects of the examined management types, the proportion of grazed sites should be promoted as it can increase diversity compared with mown sites. However, a moderate intensity and duration of grazing is crucial to preserve biodiversity. Land use as such supports grassland biocoenoses in Central Europe, prevents grasslands from scrub encroachment adding to landscape diversity in addition to forests.

Conclusion

Our well-founded data showed that the majority of Orthoptera species were 'losers', i.e. they were more common in low-intensity grasslands, which may ultimately add to their vulnerability and local extinction risk. Such negative impacts may be particularly well detectable in an analysis of individual species' land-use responses like the niche model, rather than in aggregate analyses at the community-level. Note that abundance-weighted diversity indices such as Shannon have an inherent bias for abundant species and are not sensitive for rare species, for which the probability of detection is lower than for common ones. In contrast, our new species-level niche model is very sensitive to depict quantitative responses to environmental gradients such as land use, even for rare species, and revealed that a high proportion of species declines with land-use intensity. A species' sensitivity often corresponds to its rarity, either as cause or as consequence. It is thus crucial to disentangle responses for each species with an unbiased approach, which is applicable for different organisms and environmental parameters. Our study enhances our knowledge on the susceptibility of orthopteran diversity and abundance to different types of land use in grasslands. Sustainable management, low-intensity of fertilization, infrequent mowing and variable grazing would help to maintain a high diversity of orthopterans and surely other grassland organisms.

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CHAPTER II – INTENSIVE LAND USE DRIVES SMALL-SCALE HOMOGENIZATION OF PLANT- AND LEAFHOPPER COMMUNITIES AND PROMOTES GENERALISTS

Melanie N. Chisté, Karsten Mody, Gernot Kunz, Johanna Gunczy, Nico Blüthgen

ABSTRACT

The current biodiversity decline through anthropogenic land-use not only involves local species losses, but also homogenization of communities, with a few generalized species benefitting most from human activities. Most studies assessed community heterogeneity (ß-diversity) on larger scales by comparing different sites, but little is known about impacts on ß-diversity within each habitat, which is relevant for understanding variation in the level of α-diversity, the small-scale distribution of species and associated habitat heterogeneity. To obtain our unique dataset with 36,899 individuals out of 117 different plant- and leafhopper (Auchenorrhyncha) species, we sampled communities of 140 managed grassland sites across Germany by quantitative vacuum suction of five 1 m^2 plots on each site. Sites differed in land-use intensity as characterized by intensity of fertilization, mowing and grazing. Our results demonstrate a significantly within-site homogenization of species richness of plant- and leafhopper communities, but no change in species turnover with increasing land-use intensity. Correspondingly, density (-78%) and α-diversity (-35%) declined, particularly with fertilization and mowing intensity. More than 34% of plant- and leafhopper species were significant losers and only 6% were winners of high land-use intensity, with abundant and widespread species being less affected. Increasing land-use intensity adversely affected dietary specialists and promoted generalized species. Our study emphasizes considerable, multifaceted effects of land-use intensification on species loss, with a few dominant generalists winning, and an emerging trend towards more homogenized assemblages. By demonstrating homogenization for the first time within sites, our study highlights that anthropogenic influences on biodiversity even occur on small scales.

Key words: Auchenorrhyncha, beta diversity, Biodiversity Exploratories, environmental niche, grassland land-use

INTRODUCTION

Anthropogenic land-use affects ecological communities in various ways. To estimate the impact of environmental changes on communities, responses are most commonly measured as aggregate local diversity per site (α-diversity). In addition, changes in community composition can be explored by responses of variation in species composition across sites (β-diversity) and/or on different scales. High β-diversity suggests that communities differ in their species composition between different areas. Areas can be defined as different spatial scales; communities can thus be compared between countries, regions or sites – or across small subplots within a site, as in our study. Spatial heterogeneity of communities is often evidence for a large variety of habitats, which may host various functional groups of organisms and thus enhance an ecosystem's capacity to buffer disturbances (Hooper et al. 2005). A high diversity of species in an ecosystem is favoured by diverse landscapes (Atauri and Lucio 2001, Tscharntke et al. 2012, Gámez-Virués et al. 2015), with a variety of microhabitats

available for different requirements (Anderson 1978). This landscape aspect is likely to be applicable also to smaller scales. Disturbances – such as agricultural land use – lead to a loss of these diverse habitats, with the trend to large-scale monocultural farming and similar treatment of large areas causing impoverishment of ecosystems. This can appear as diversity loss (Haddad et al. 2000, Kleijn et al. 2009), loss of ecosystem functions (Flynn et al. 2009), degradation of soil and water (Foley et al. 2005) and homogenization of communities (Gossner et al. 2016). Homogenization of communities due to disturbance has often been described for animals (Dormann et al. 2007, Ekroos et al. 2010), as well as for plants (Schulte et al. 2007). Homogenization was measured in many cases as the difference in community composition between sites (Dormann et al. 2007, Ekroos et al. 2010, Knop 2016, van der Plas et al. 2016, Gossner et al. 2016), but not as homogenization within sites. More investigations on within-site homogenization are needed, as sites may show considerable small-scale heterogeneity of microhabitats, which is known, for example, from grazed sites (Jaramillo and Detling 1992) or semiarid ecosystems (Maestre et al. 2003). Small-scale environmental variation influences species assemblages (Blanchet et al. 2013, Horn et al. 2015), and segregation of assemblages within sites may promote a higher level of α-diversity (García-Tejero and Taboada 2016), for example by competitive release. For butterflies, small scale landscape heterogeneity can promote α-diversity (Weibull et al. 2000).

Anthropogenic land-use is an important driver of landscape and habitat homogenization. Through increased homogenous treatment of large areas and monocultural cultivation, landscapes become more equal and microhabitat quality and diversity decreases. In grasslands, especially mowing intensity drives homogenization of multitrophic communities (Gossner et al. 2016). Homogenization and loss of diversity in grassland communities due to land use have been reported frequently, while studies cover examination of different scales (Scott and Helfman 2001, Rodrigues et al. 2013, Gossner et al. 2016). Heterogeneity of species composition at a large spatial scale is as important as diversity on single sites to gain multiple ecosystem functions (van der Plas et al. 2016). High diversity of these functions, which can be achieved by high species diversity, is likely to increase ecosystem stability (Naeem and Li 1997).

With increasing land-use intensity, diversity of different taxa decreased (Allan et al. 2014), among others of herbivorous insects (Andrey et al. 2016, Chisté et al. 2016). Herbivorous insect diversity is especially dependent on a diverse selection of food plants, and thus decreases when plant diversity declines (Scherber et al. 2010), which is a process promoted by intensive land use (Socher et al. 2013). Plant- and leafhoppers belong to the most abundant insect herbivores in grassland ecosystems and may show densities of more than 1000 individuals per square meter (Nickel et al. 2002). At the same time, they are sensitive to environmental deterioration (Nickel and Hildebrandt 2003, Biedermann et al. 2005, Knop 2016). In Germany, 40% of the species are listed on the red list of endangered species, thereof 10 % are critically endangered (Nickel et al. 2016).

In Germany more than 220 species feed on Poaceae, the rest of the 620 recorded species of Germany

are feeding on other grasses (Cyperaceae, Juncaceae), herbs, shrubs, trees, ferns and fungi with variable degrees of host specificity (Nickel 2003). To show within-site community differences, plant- and leafhoppers thus should provide a highly suitable study system. In Switzerland, a large-scale homogenization of leafhopper communities due to urbanization could be shown (Knop 2016).

We studied the response of plant- and leafhopper communities to a gradient of land-use intensity, pursuing the following objectives:

(1) To determine the effects of land-use intensity on the plant- and leafhopper community by quantifying the response of density and α-diversity. As plant- and leafhoppers have been found to be suitable indicators of disturbance (Nickel and Hildebrandt 2003, Biedermann et al. 2005, Wallner et al. 2013, Knop 2016), we expected negative effects of increasing land-use intensity on the community.

(2) To disentangle the variable responses of different species to land-use intensity by performing a species-level analysis, which provides information on possible selectivity of species concerning land-use intensity. We hypothesize negative effects of increasing land-use intensity on the single species level with a high proportion being loser species.

(3) To find out whether high land-use intensity changes the proportion of dietary generalists in contrast to dietary specialists in the community. Dietary specialists were expected to decline according to findings for other taxa (McKinney and Lockwood 1999).

(4) To test if high land-use intensity leads to community homogenization (in terms of species richness and turnover) at a small scale, and to clarify whether β-diversity is represented by local species loss (nestedness) or local replacement of species (turnover). Based on a standardized density sampling, using five independent plots on each site, it was possible to examine the response of within-site heterogeneity to land-use intensity. We hypothesize community homogenization with increasing land-use intensity, as it has been shown on the between-site scale for multiple taxa (Gossner et al. 2016).

MATERIALS & METHODS

Our studies were part of the Biodiversity Exploratories (Fischer et al. 2010), which is a research project existing since 2008 and includes three regions across Germany: the biosphere reserve Schwäbische Alb in the south-west (ALB, 48°43'N 9°37'E, 460–860 m a.s.l., area about 420 km^2, annual mean precipitation 700–1000 mm, mean annual temperature 6–7 °C), national park Hainich-Dün and surrounding areas in the centre (HAI, 51°20'N 10°41'E, 285–550 m a.s.l., 1300 km^2, 500–800 mm, 6.5–8 °C) and biosphere reserve Schorfheide-Chorin in the north-east (SCH, 53°02'N 13°83'E, 2–139 m a.s.l., 1300 km^2, 500–600 mm, 8–8.5 °C). Each region has 50 grassland sites, which represent a gradient of land-use intensity, defined by the frequency of mowing (cuts • $year^{-1}$), the amount of applied fertilizer (kg N • ha^{-1} • $year^{-1}$) and the intensity of grazing (livestock units • grazing days • ha^{-1} • $year^{-1}$). Each site is specified by its index of land-use intensity (LUI), which combines the

three land-use components (Blüthgen et al. 2012) and is calculated as

$$LUI_S = \sqrt{\frac{F_s}{F_r} + \frac{M_s}{M_r} + \frac{G_s}{G_r}}$$

where intensities of fertilization (*F*), mowing (*M*) and grazing (*G*) on site *s* is standardized by the mean global intensity of all regions (*r*). Land-use information is gained annually by interviews with the landowners and farmers.

In July and August 2015, we sampled 140 grassland sites (50 m x 50 m) in the three regions (ALB: 48, HAI: 49, SCH: 43), using a suction sampler, which was a modified leaf vacuum (Stihl SH 86, Andreas Stihl AG & Co. KG, Germany) with an interposed gauze catcher. Along a transect of 200 m, five randomly chosen square meters (in the following: plots) were sampled with a biocenometer, an aluminium frame (1 m × 1 m area, height 0.6 m) covered with gauze (Chisté et al. 2016). Combining this biocenometer with the suction sampler allowed standardized plant- and leafhopper sampling, not only in the herb, but also in the ground layer. All 45,987 plant- and leafhopper individuals were checked for species identity and determined to the species level where possible by G. Kunz with a combination of identification literature (Holzinger et al. 2003, Biedermann and Niedringhaus 2004, Kunz et al. 2011, Stöckmann et al. 2013). We excluded undetermined nymphs from the analyses. Some individuals could be identified to genus level only. If no congeneric species have been identified on the same site, they were treated as a single species. If one or more congeneric species occurred in the same biocenometer, the unidentified individuals were allocated to the most common species. *Fieberiella* spec and *Platymetopius* spec were treated as species in the analysis as they were the only representatives of their genus in the whole study area. A total of 36,899 individuals remained for the analysis.

Data analysis

We used the available land-use data of the year 2014 and square-root transformed the raw data of fertilization and grazing intensity and abundance data in all analyses, to homogenize data distribution. Statistical analyses and graphs were made with R version 3.2.2 (R Core Team 2015). To estimate the representativeness of our sampling, we calculated Chao 1 richness estimators (Chao 1984) with EstimateS version 9.1.0 (Colwell 2013) to assess the deviation from the expected species number in each region and in each site, respectively.

As communities are assembled of many rare and only a few common, dominant species, we were interested in the responses of rare and common species equally. To avoid an analysis where the effects on common species overlay the effects on rare species, like in abundance- weighted diversity indices, we have chosen species richness as main response variable. To not completely ignore an abundance-weighted effect of land-use intensity on diversity, we additionally analysed the response of Shannon and Simpson indices (see supplementary material).

For comparison of community composition within-site (between plots) we chose β-diversity as a comprehensible measure of heterogeneity. β-diversity was calculated subtracting α-diversity (within plot) from γ-diversity (within site), which is known as additive partitioning (Veech et al. 2002). This approach gives information about the differences in diversity of the single plots to the whole-site diversity. We used different approaches defining β-diversity based on the Hill numbers *q* (Hill 1973), where α-diversity can represent species richness (*q* = 0, α_{SR} or β_{SR}), effective Shannon diversity (*q* = 1, α_{SHA} or β_{SHA}) or inverse Simpson diversity (*q* = 2, α_{SIM} or β_{SIM}). With increasing Hill number from β_{SR} to β_{SIM}, rare species obtain less weight. We used effective numbers of species (effective Shannon $e^{H'}$, inverse Simpson $1/(1-H_{GS})$ for α and β, which is a common practice to obtain indices that are more comprehensible by showing the same unit as for species richness (Chao et al. 2014). β-diversity can be partitioned into nestedness (communities are subsets of each other) and total species turnover (community differences through species replacement) (Baselga 2010). Partitioning was performed using the R package 'betapart' (Baselga et al. 2013), with β-diversity, describing the proportion of species shared between plots within each site (n = 140). β-diversity within each site was decomposed into nestedness and turnover. Turnover can be a measure of β-diversity, representing β-diversity independently from α-diversity.

We used linear modelling to analyse average density per square meter (= total abundance/5), α_{SR}, α_{SHA}, α_{SIM}, β_{SR}, β_{SHA}, and β_{SIM}, and species turnover within sites in response to region and LUI, fertilization, mowing or grazing intensity in single models, regarding also the interaction of the region with one of our predictors. To simplify display of species and density loss or gain, we calculated percentage loss/gain from a regression curve and therefore disregarded the effect of region, where we wanted to reflect the raw effect of land-use intensity. For the α-scale, we refer to the site scale (i.e. total species richness per site), while the β-scale compares the five plots within a site.

We counted those individuals that were identified to the genus level only and occurred as the only representatives of this genus on the site (but not in the whole study area) as own species on this site. Species were categorized into dietary groups that differed in dietary specialization according to Nickel (2003), where 'm1' specialists feed on one plant species, 'm2' on one plant genus, 'o1' on one family, 'o2' on two families or four species of different families and 'p' on a broad spectrum of plants. We analysed the proportion of species that belong to dietary group m1, m2, o1, and p as depending on compound land-use intensity by linear modelling. We excluded species for which specialization was unknown and species of dietary group o2, where number of samples was too small (four species) for statistical analysis.

To understand land-use effects on the species level, we calculated a 'land-use niche' for each species and analysed the data with a randomization approach (Chisté et al. 2016). The niche analysis is sensitive to the land-use response of rare species. In addition to diversity measures, which express the response of whole communities, our niche-model depicts responses of single species.

The 'niche optimum' of a species was defined as

$$\mu_i = \sum_{s=1}^{140} p_{i,s} \cdot L_s$$

where μ_i is the abundance-weighted mean of species i, p is the proportion of species i on site s (in relation to its total abundance on all sites) and L is the land-use intensity on site s. The 'niche breadth' of each species was reflected by the abundance-weighted standard deviation (σ_i). In a null model we assumed that each species could choose each site (only within the region they occurred) along the land-use intensity gradient with the same probability. With an iteration of 10,000 we calculated an expected μ_i. This computation considers the number of sites each species occurred, e.g. for a species with a site occurrence of 20, the null model 10,000 times picks out 20 different sites (an thus land-use intensities). Each expected μ_i is compared with the observed μ_i, resulting in a p-value that predicts deviation from the null model. Species are categorized as 'winners' of intensive land use, when their observed μ_i is significantly smaller than their expected μ_i, or as 'losers', when their observed μ_i is significantly greater than their expected μ_i. Moreover, to quantify niche breadth (and to allow detecting specialists of intermediate land-use intensity), we computed the coefficient of variation ($CV_i = \sigma_i/\mu_i$) of the observed and the expected weighted means. Species that were specialists of intermediate land-use intensity would thus have an observed μ_i similar to expected, but an observed CV smaller than expected and not zero (species with only one site occurrence, because $\sigma_i = 0$). To demonstrate whether the results depend on rare species, we repeated the analysis after exclusion of species occurring on fewer than 5 sites, and those having total abundances lower than 10 (see supplementary material, Table S 3.3).

To examine if species with higher μ_i are those species that are more abundant and more common, we related the μ_i of LUI and the three individual land-use components to total species abundance and to site occurrences and tested this relationship with Pearson's product-moment correlation.

RESULTS

We identified 117 species (n = 38,945 individuals) of plant- and leafhoppers in our samples. The host plant specificity was as follows: 28 species are known to feed on a single plant species (monophagous; m1), 16 species on a single genus (m2), 35 species on several genera from a single plant family (oligophagous; o1), 4 species on two families or up to four species of different families (o2), and 24 species on a broad spectrum of plants (polyphagous; p); the host plant specificity of the remaining 20 species is unclear. Based on Chao1 we found 87% of the estimated species in all regions, 88% in region ALB, 92% in region HAI and 96% in region SCH. On the site-level we found on average 82% (± 16.7 sd) of the estimated species.

Density and α-diversity

Density of plant- and leafhopper (individuals per m^2) was strongly affected by compound land-use intensity (LUI), fertilization and mowing. In general, density was significantly higher on unfertilized than on fertilized sites (boxplot Fig. 3.1a; $F_{1,134} = 6.4$, $P = 0.012$). Specifically, density decreased by 78% from the lowest to the highest LUI across sites, by 40% from unfertilized to most intensively fertilized sites and by 32% from unmown sites to most frequently mown sites (Fig. 3.1a; LUI: $F_{1,134} = 8.3$, $P = 0.006$; fertilization: $F_{1,134} = 5.8$, $P = 0.018$; mowing: $F_{1,134} = 5.6$, $P = 0.02$). Although a similar trend along the range of grazing intensity (-31%), the effect was not significant ($F_{1,134} = 0.4$, $P = 0.555$).

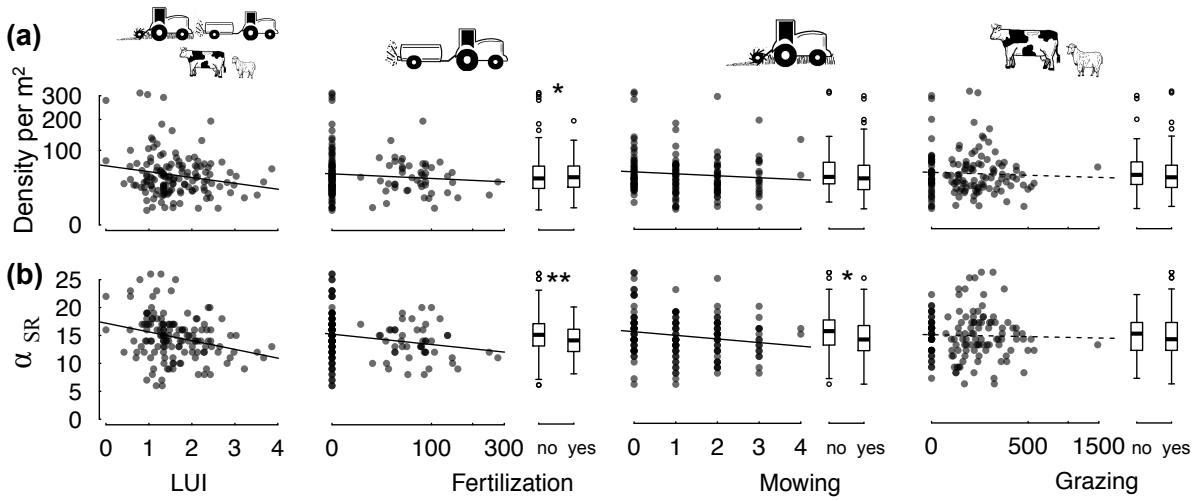

Figure 3.1: Land-use effects on plant- and leafhopper density and α_{SR} (Species richness) of each site. We show effects of compound land-use intensity (LUI), fertilization (kg N × ha^{-1} × $year^{-1}$), mowing (cuts × $year^{-1}$) and grazing intensity (livestock units × grazing days × ha^{-1} × $year^{-1}$) on (a) density per m^2 and on (b) species richness α_{SR}, of each site (n = 140). In boxplots, sites are partitioned into unfertilized, unmown or ungrazed (no) and fertilized, mown and grazed sites (yes); significant relationships are indicated by asterisks (boxplots; *$P < 0.05$; **$P < 0.01$), or by solid lines (scatterplots). Data were analysed by linear modelling with region and land-use intensity as predictors.

Species richness (α_{SR}) of plant- and leafhoppers was also affected by land-use intensity. Increasing LUI strongly reduced (-35%) species richness ($F_{1,134} = 11.6$, $P < 0.0001$). Fertilized and mown sites had significantly fewer species than unfertilized and unmown sites (boxplot Fig. 3.1b; fertilization: $F_{1,134} = 6.9$, $P = 0.009$; mowing: $F_{1,134} = 6.3$, $P = 0.014$). Species richness declined by 40% along the range of fertilization intensity and by 31% along the range of mowing intensity (Fig. 3.1b; fertilization: $F_{1,134} = 7.9$, $P = 0.006$; mowing: $F_{1,134} = 5.3$, $P = 0.023$). Grazing intensity (-4%) did not significantly reduce species richness ($F_{1,134} = 0.04$, $P = 0.84$).

Neither effective Shannon diversity nor inverse Simpson diversity were significantly affected by LUI or one of the three individual land-use components (Supplementary material, Fig. S 3.1 and Table S 3.1).

Losers and winners of high land-use intensity

More than a third of the plant- and leafhopper species recorded in our study were significant losers

of intensive land use (LUI), i.e. they were more abundant on low-intensity sites (Table 3.1, Fig. 3.2, more detailed in supplementary material, Table S 3.2). Only a small percentage of the analysed species were winners of intensive land use. We found a large proportion of losers of intensive mowing, followed by fertilization. Numbers of losers and winners of intensive grazing were similar. Half of the species were found only on unfertilized sites (Table 3.1).

As expected, we found a significant positive correlation of niche breadth (σ_i) and niche optimum (μ_i) of the species (r = 0.350, $P < 0.001$). Most of the species with small niche breadth (σ_i, see Fig. 3.2) occurred with higher abundances on low-intensity sites, i.e. their μ_i was located on the left side of the dashed line in Figure 3.2. When excluding species with low site-occurrences and low total-abundances, the proportion of losers and winners increased for LUI and the single management types (see supplementary material, Table S 3.3).

More abundant species (sum of all abundances across all sites) had significantly higher niche optima for compound land-use intensity LUI than rare species (r = 0.262, $P = 0.004$). Such a positive correlation was also confirmed for fertilization (Fig. 3.3; r = 0.264, $P = 0.004$) and for mowing (r = 0.263, $P = 0.004$), but not for grazing intensity (r = -0.054, $P = 0.56$). In addition, the species' niche optimum increased with their distribution (number of sites in which they occurred). This was true for LUI (Fig. 3.3; r = 0.419, $P < 0.001$), fertilization (r = 0.376, $P < 0.001$) and mowing (r = 0.364, $P < 0.001$), but again not for grazing intensity (r = -0.014, $P = 0.878$).

Table 3.1: Number of plant- and leafhopper 'loser' and 'winner' species of intensive land use. We calculated abundance-weighted means ($\mu_{i,obs}$) of compound land-use intensity (LUI), fertilization (kg N × ha^{-1} × year^{-1}), mowing (cuts × year^{-1}) and grazing intensity (livestock units × grazing days × ha^{-1} × year^{-1}) for each species. If this observed niche optimum ($\mu_{i,obs}$) was significantly smaller than expected ($\mu_{i,exp}$) by the null model with a randomization approach, we named these species 'losers'. If the relationship was vice-versa, species were named 'Winners' ($\mu_{i,obs} > \mu_{i,exp}$). Species with no significant deviance from the null model (Neutrals) were partitioned into those with smaller $\mu_{i,obs}$ than $\mu_{i,exp}$ (occurring mainly on low intensity sites), and those with greater $\mu_{i,obs}$ than $\mu_{i,exp}$ (occurring mainly on high intensity sites). Species that only occurred on sites with no land use ($\mu_{i,obs} = 0$) can be neutral or significant losers. We show total abundances and percental abundances of all 117 plant- and leafhopper species.

	Losers		**Winners**	**Neutrals**	
	$\mu_{i,obs} = 0$	**$\mu_{i,obs} < \mu_{i,exp}$ ($p<.05$)**	**$\mu_{i,obs} > \mu_{i,exp}$ ($p<.05$)**	$\mu_{i,obs} < \mu_{i,exp}$	$\mu_{i,obs} > \mu_{i,exp}$
LUI	0	**40 (34.2%)**	**7 (6%)**	53 (45.3%)	17 (14.5%)
Fertilization	55 (47%)	**17 (14.5%)**	**7 (6%)**	79 (67.5%)	14 (12%)
Mowing	26 (22.2%)	**33 (28.2%)**	**11 (9.4%)**	55 (47%)	18 (15.4%)
Grazing	6 (5.1%)	**11 (9.4%)**	**6 (5.1%)**	49 (41.9%)	51 (43.6%)

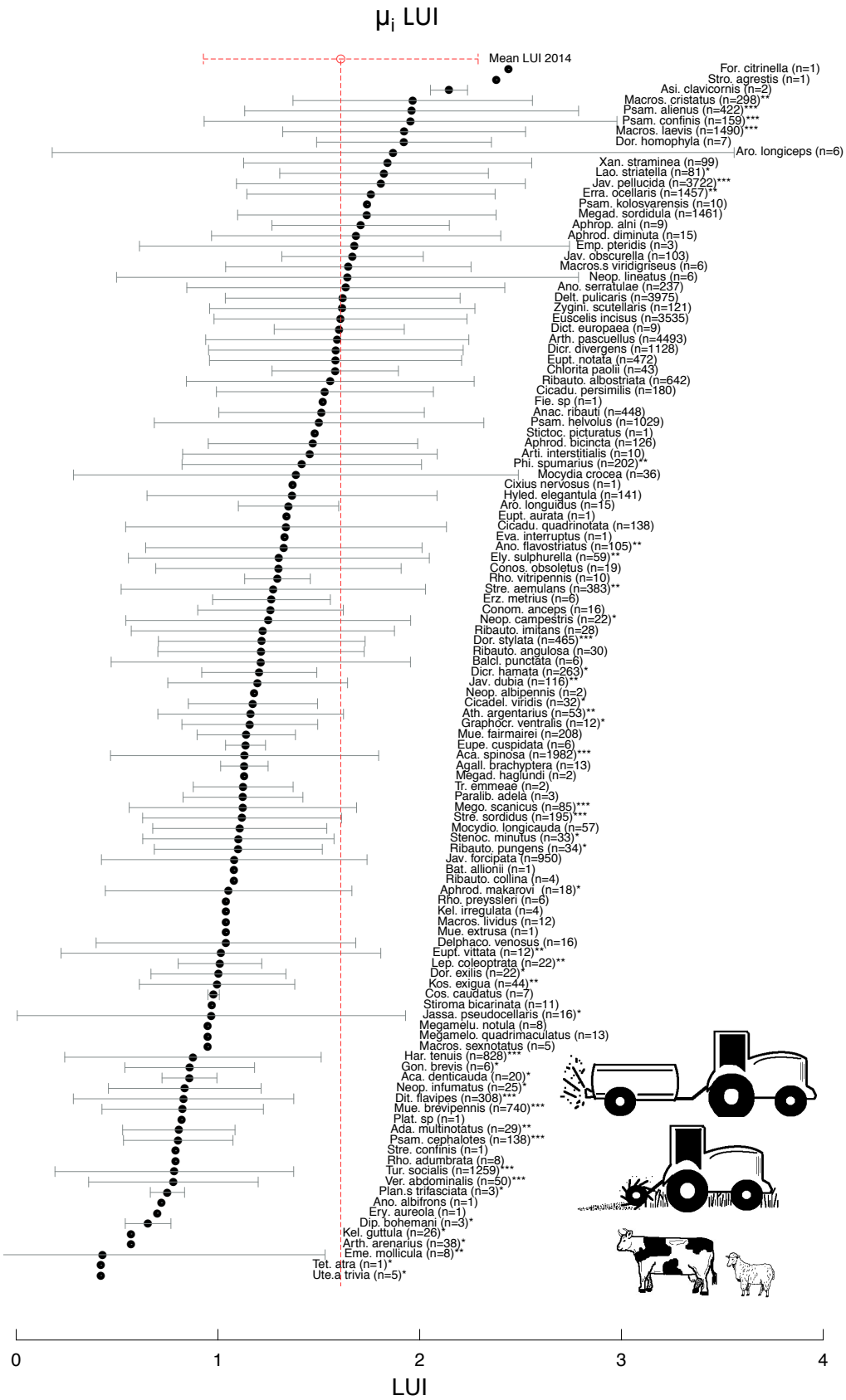

Figure 3.2: Land-use intensity niches of plant- and leafhopper species. We show abundance-weighted means (μ_i; circles) of land-use intensity index (LUI) for each species with weighted standard deviation (σ_i), representing the species' niche breadth. Mean land-use intensity in 2014 with standard deviation across all sites and regions is illustrated by the vertical dashed line, and is a proxy for the weighted mean, expected by the null model by a randomization approach. Significant deviations from the expected means are starred; starred species on the right side of the dashed line are characterized as 'winners', while on the left side are characterized as 'losers' of intensive land-use; total abundance of each species is shown in parentheses. See supplementary material for full species names.

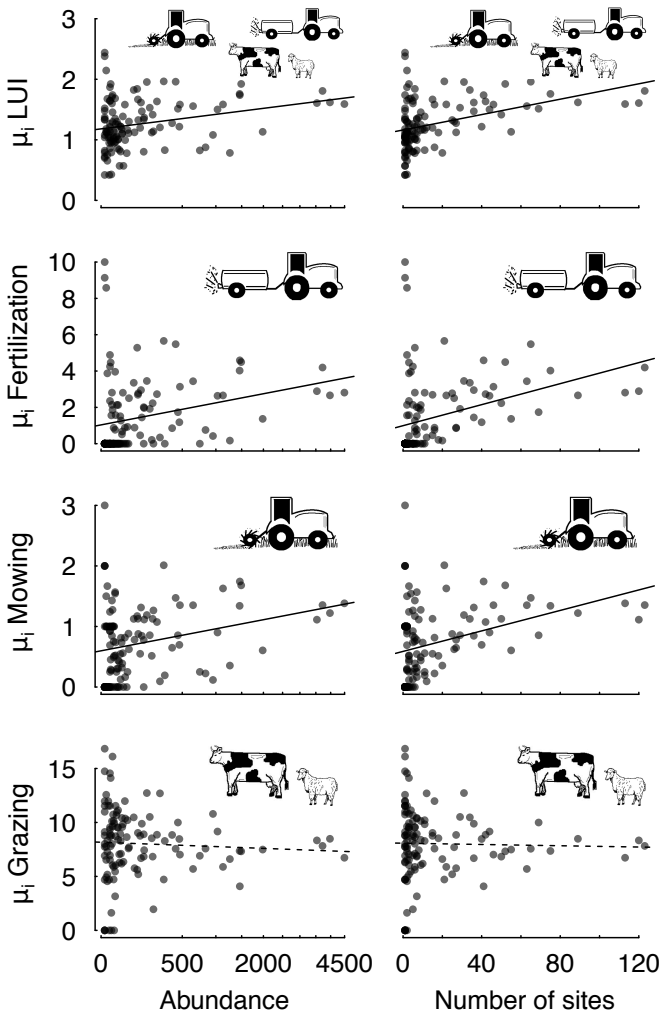

Figure 3.3: Correlation of land-use niches (Fig. 3.2) with species' total abundance and the number of sites (n = 140) they occurred. We show the abundance weighted means (μ_i) of each species i in correlation with its total abundance on all sites (Abundance) and the number of sites it occurred in all regions. Solid lines indicate significant correlations (with r < 0.25 and P < 0.01) by Pearson's product-moment correlation; abundances are square-root transformed.

Responses of generalists and specialists to land-use intensity

Intensive compound land-use intensity (LUI) reduced the proportion of strictly monophagous species (m1, Fig. 3.4; $F_{1,109} = 8.5$, $P = 0.004$) and of species feeding on one plant genus (m2, $F_{1,82} = 21.1$, $P < 0.001$). The proportion of oligophagous species did not change consistently with LUI (o1, $F_{1,138} = 2.9$, $P = 0.089$), whereas the proportion of polyphagous species increased (p, $F_{1,137} = 9.6$, $P = 0.002$).

β-diversity

Mean β_{SR}-diversity (based on richness) of each site decreased (-33%) with increasing compound land-use intensity LUI (Fig. 3.5; $F_{1,134} = 6.5$, $P = 0.012$; supplementary material, Table S 3.4). However, mean β_{SR} was not affected by increasing fertilization, mowing or grazing intensity alone (fertilization: $F_{1,134} = 3.6$, $P = 0.06$; mowing: $F_{1,134} = 2.2$, $P = 0.138$; grazing: $F_{1,134} = 0.2$, $P = 0.585$), though declined by 20% with fertilization, by 15% with mowing, and by 6% with grazing intensity. We found a significant interaction of mowing and region on β_{SR} ($F_{2,134} = 3.4$, $P = 0.038$), where mowing intensity had no effect in the regions ALB ($F_{1,46} = 0.1$, $P = 0.773$) and SCH ($F_{1,41} = 0.1$, $P = 0.757$), whereas there was a significant negative effect in HAI ($F_{1,47} = 6.7$, $P = 0.013$).

We found trends of decreasing mean β_{SHA} and mean β_{SIM} but no significant relationships, whereas trends were stronger for β_{SHA} than for β_{SIM} (detailed results in Supplementary material, Fig. S 3.2 and Table S 3.4).

Decomposition of β-diversity on the plot scale showed that β_{SR} reflected more species turnover (mean ± sd: 80.79% ± 11.63%) than nestedness (19.21% ± 11.63%). The proportion of species turnover was not influenced by LUI (Fig. 3.5b; $F_{1,140} = 0.01$, $P = 0.912$), but there was a significant interaction of turnover with region ($F_{1,140} = 4.79$, $P = 0.01$). In region ALB species turnover increased with increasing LUI ($F_{1,48} = 5.98$, $P = 0.018$), and was not affected in HAI ($F_{1,49} = 3.19$, $P = 0.081$) and SCH ($F_{1,43} = 0.27$, $P = 0.606$). Fertilization intensity had no effect on species turnover ($F_{1,140} = 0.76$, $P = 0.385$), neither had mowing intensity ($F_{1,140} = 1.8$, $P = 0.183$). We found a significant interaction of mowing and region; in ALB mowing frequency had positive effects on species turnover within the sites ($F_{1,48} = 7.22$, P = 0.01), while it had no effects in region HAI ($F_{1,49} = 2.49$, $P = 0.121$) and SCH ($F_{1,43} = 0.35$, $P = 0.56$). Grazing had no effect on species turnover ($F_{1,140} = 0.24$, $P = 0.628$; results in detail are provided in supplementary material Table S 3.5).

Overall, there was a strong correlation between β- (mean per site) and α-diversity (whole-site diversity) across the 140 sites (r = 0.864, $P < 0.001$) and between β-diversity and density per site (r = 0.185, $P = 0.029$). Species turnover per site was not correlated with α-diversity (whole-site diversity; r = 0.014, $P = 0.634$), but was negatively correlated with density per site (r = -0.405, $P < 0.001$).

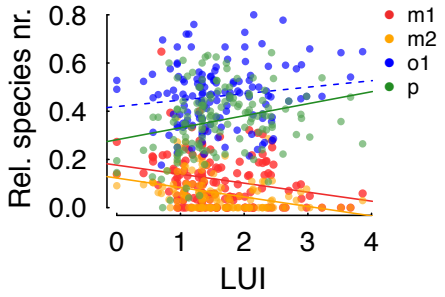

Figure 3.4: Relative numbers of species on grassland sites (n = 140), which are feeding only on one plant species (m1), on one genus (m2), on one family (o1) or on a broad spectrum of plants (p) along a gradient of land-use intensity (LUI). Solid lines indicate significant relationships, which were tested by linear modelling. Species numbers are relative to total species numbers on sites. The second oligophagous category (o2) is not displayed because it only contained four species in total.

DISCUSSION

Land-use intensity, particularly fertilization and mowing, showed a negative effect on both the density and diversity of plant- and leafhoppers. Apart from confirming this effect, which has been reported for other taxa in the same project (Allan et al. 2014, Simons et al. 2014, Chisté et al. 2016) and elsewhere (Haddad et al. 2000, Humbert et al. 2010) for plant- and leafhoppers, our results revealed for the first time that insect communities in grasslands become more homogenous in species richness, but not in species turnover within each site and that dietary specialists become rarer with increasing land-use intensity.

Land-use effects on density and α-diversity

The diversity of different insect taxa has been regularly found to decrease due to intensified land-use (Haddad et al. 2000, Nickel and Hildebrandt 2003, Allan et al. 2014), and has also been reported for plant- and leafhoppers (Nickel and Hildebrandt 2003, Wallner et al. 2013, Andrey et al. 2016). In contrast, insect abundance seems to rather ambiguously respond to land-use intensification. These responses can be neutral (Chisté et al. 2016), positive (Haddad et al. 2000, Hudewenz et al. 2012) or negative (Humbert et al. 2010, Hudewenz et al. 2012), which was also the case in our study.

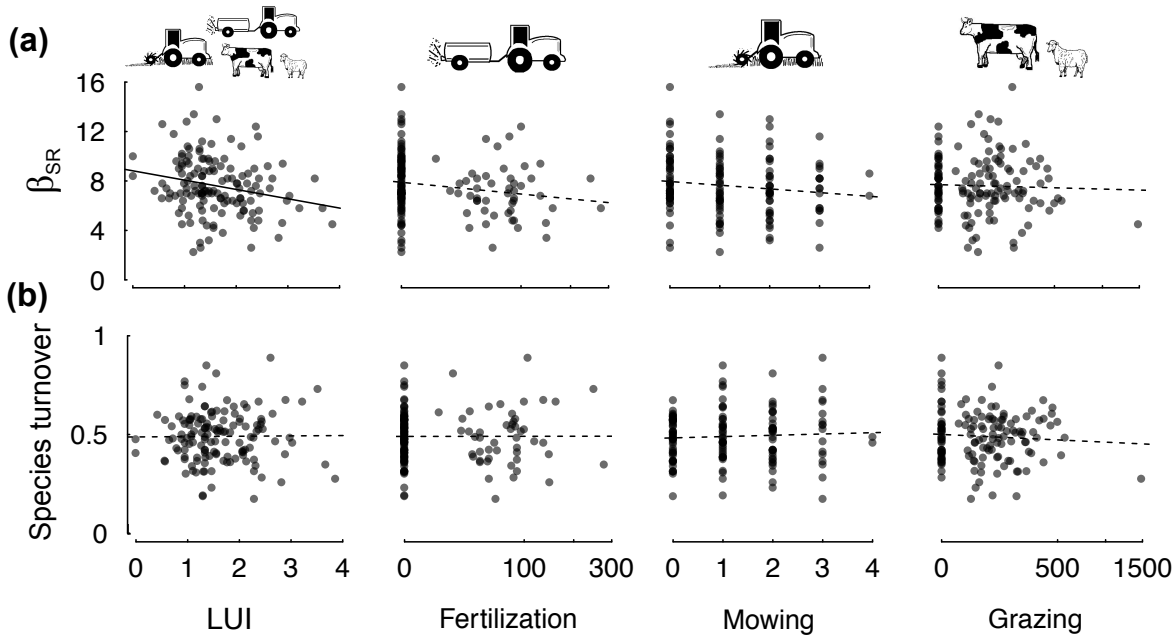

Figure 3.5: Land-use intensity effects on (a) mean (of five randomly chosen plot samples of each site) plant- and leafhopper β_{SR} (changes in species richness between plots) within-site and on (b) species turnover (changes in community composition between plots) between the plots within each site. Explanatory variables are compound LUI, fertilization intensity (kg N × ha^{-1} × $year^{-1}$), mowing intensity (Cuts × $year^{-1}$) and grazing intensity (livestock units × grazing days × ha^{-1} × $year^{-1}$). Solid lines indicate significant relationships tested by linear modelling with region and land-use intensity as predictors.

In our study, fertilization and mowing had negative effects on density and diversity of plant- and leafhoppers, while grazing did not affect the communities. Nitrogen input and mowing reduces plant species richness (Kleijn et al. 2009, Socher et al. 2012), which has also been confirmed for our study sites (Socher et al. 2012, 2013, Simons et al. 2014, Gossner et al. 2016). As many plant- and leafhopper species are monophagous on single plant species or genera (almost 40% of the species in our study), the loss of plant species richness can easily cause a loss of plant- and leafhopper species. Intensified mowing causes strong changes in habitat characteristics (changes in climate, humidity, food availability, predation pressure), and increases the mortality of herbivorous insects on meadows (Humbert et al. 2009). Grazing is a spatially and temporally more heterogeneous way of grassland maintenance than mowing, which can create new microhabitats by trampling down or cutting out patches, or providing differently fertilized spots by random provision of animal faeces on pastures. This might be a reason why grazing had no effects on the plant- and leafhopper community in the present study.

Losers and winners of high land-use intensity

Our analyses of land-use niches, representing each species' selectivity along the land-use gradient, strongly supported the evidence that a large proportion of species is impaired by intensive land use. Many species were found only on low intensity sites; a large proportion of species only occurred on sites with no fertilization or mowing.

Most species were either loser or winner of the overall land-use intensity gradient or the individual land-use components. Abundant and widespread species (high local density and wide occurrence, respectively) were also more tolerant to high land-use intensity than rare species. Their land-use tolerance may thus be a main prerequisite for their success in cultural landscapes. Through changes in habitat structure, plant community composition and disturbance frequency, shifts in the competitive ability in the plant- and leafhopper community could lead to a higher dominance of particular species. The high susceptibility of rare species to land-use intensity demonstrates that it is worthwhile to zoom into the community and take into account single species responses in addition to the aggregate community level. In comparison to some weighted approaches to describe diversity and community composition, the niche model used here is very sensitive for detecting responses of rare species (Chisté et al. 2016), which may play important roles in grassland ecosystems (Soliveres et al. 2016).

Macrosteles laevis showed up as a winner of high LUI, strong fertilization and frequent mowing and was one of the most abundant species. Other studies showed accordingly that this species thrives where other species decline (Morris et al. 2005, Nickel and Achtziger 2005). Older research on the selectivity of German plant- and leafhoppers along a gradient of land-use intensity showed similarities and dissimilarities with our results (Nickel and Achtziger 1999). Accordingly we found pioneer species like *Macrosteles cristatus* and *Psammotettix alienus* to be tolerant to intensive land use, whereas *M. cristatus* had a very narrow niche breadth and was not found on extensive grasslands. *Chlorita paolii*, which is known to prefer unused and ruderal sites, and *Mocydia crocea*, which is known to prefer extensive sites, were found in our study to be neutral and not to have special land-use preferences. The affiliation of *Emelyanoviana mollicula*, *Kelisia guttula* and *Doratura exilis* to rather extensive sites could be confirmed in the present study.

Responses of generalists and specialists to land-use intensity

Species that are specialized to variable degree towards different ecological parameters, such as habitat specificity (Devictor et al. 2008, Ekroos et al. 2010), voltinism, dispersal ability (Börschig et al. 2013) or feeding specificity (McKinney and Lockwood 1999), decrease in strongly cultivated landscapes. In strongly managed sites, communities of plant- and leafhoppers were less diverse and dominated by generalized species (Nickel and Hildebrandt 2003), which corresponds to our findings. Dietary specialists decreased and generalists increased with increasing land-use intensity. This trend might be caused by similar reasons as the decline in α-diversity and the large proportion of losers with increasing land-use intensity. Generalists often have the advantage of being more widespread, highly

variable, more dispersive and eurytopic (McKinney and Lockwood 1999).

From species richness, via Shannon to Simpson entropy, common species are weighted increasingly, which means that (at least local) rare species are increasingly neglected in the analysis. For the community-level analyses we detected the strongest effects of land-use intensity on species richness and only weak trends for Shannon and Simpson diversity. This finding corresponds to the species-level analysis, showing that rare species are particularly strong losers of land-use intensity whereas a few dominant species are the only winners.

Community homogenization

Our study showed that, on a small scale within the sites, land-use intensification homogenizes plant- and leafhopper communities with regard to species richness, but not to species turnover. Intensive management leads to increased similarity of plot species-richness and whole-site species richness of plant- and leafhopper communities, which is a type of biotic homogenization. Effective and large-scale homogenous management may have probably caused increased homogeneity of the study sites with increased land-use intensity. Fertilization leads to homogenization of plant communities (Schulte et al. 2007) and mowing reduces plant diversity (Socher et al. 2012), which in turn affects herbivorous insects, especially host plant specialists. The studied plant- and leafhopper communities contain many monophagous species that are adversely affected by land-use intensity. For our study sites decreases in plant diversity (Socher et al. 2013, Simons et al. 2014, Gossner et al. 2016) and homogenization of plant communities (Gossner et al. 2016) with increasing land-use intensity were demonstrated. Our finding that land-use intensification decreases the proportion of dietary specialists and increases the proportion of generalists fits to these observations.

One important process behind homogenization of communities is the local species extinctions and thus replacement by other (Rahel 2002). Susceptible species (i.e. ‘losers’ in this study) can also be replaced by species that are more tolerant against disturbance (‘winners’) and more generalized (McKinney and Lockwood 1999, Devictor et al. 2008, Ekroos et al. 2010). In this study, β-diversity represents mainly species turnover, which means that the species pools within plots differ through species replacements. Such replacements were not pronounced along the land-use gradient in our study, since polyphagous and land-use tolerant species dominated the intensively managed sites but also occurred on low-intensity sites. Common species thus seem to be shared between compared areas and differences are caused by rare species. In fact, a reduced within-site β-diversity may be one of the main drivers of losses in whole-site diversity or vice-versa, as both diversities were not independent from each other. Increasing density increased within-site β-diversity, but decreased species turnover within the sites. That is, the more plant- and leafhoppers colonize a site, the higher are the richness differences between plot to the total site-richness. However, the probability to find different species in two plots decreases. In the context of a densely populated site, a steady pool of species might explain small-scale compositional differences.

Conclusion

Our findings demonstrate that plant- and leafhopper communities are negatively affected by high land-use intensity, especially by fertilization and mowing, and that most species are losers of strong land use, with rare species being less tolerant to high land-use intensity. Based on a large dataset we demonstrated community homogenization at a small scale (within sites) concerning species richness with no influence on species turnover. Moreover, dietary generalists increased whereas specialists declined. Remarkably, we did not detect effects on abundance-weighted diversity indices, whereas species richness as well as species-level analyses revealed strong impacts of land use, i.e. a large proportion of species were significant losers and only a few widespread and common species were winners of high land-use intensity. Our results highlight that it is worthwhile approaching the susceptibility of a community at different levels, and we encourage researchers to consider within-site heterogeneity and possibly detect similar effects for other taxa. For our understanding of the complexity and potential hidden fragility of communities and ecosystems under anthropogenic influence, rare species deserve more attention.

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CHAPTER III – FERTILIZATION-MEDIATED CHANGES IN GRASSHOPPER DIETARY PREFERENCE, PERFORMANCE AND FOOD UTILIZATION

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ABSTRACT

Land-use change in grasslands is associated with an increase of nitrogen application, which has effects on diversity and performance of primary producers. The next trophic level in turn is directly affected by these alterations. Herbivorous insects can benefit or have disadvantages from N application, which is reflected by herbivore preference and performance responses to fertilization. Both responses of consumers are usually considered separately, but there is evidence for positive preference-performance relationships.

In this study we investigated the effects of different fertilization regimes on preference and performance of European Gomphocerinae grasshopper species (*Pseudochorthippus parallelus, Chorthippus dorsatus, C. biguttulus*). Experimental plots planted with *Dactylis glomerata* (orchardgrass) were treated with N and NPK fertilizer (high N treatment), with manure (low N treatment) and left unfertilized (control). Preference was recorded for each nymphs and adult grasshoppers, which were provided for 24 h with three differently treated grasses. Performance was measured for nymphal Gomphocerinae in an eleven-day feeding trial, where the animals were fed with only one of the four treated grasses. We recorded survival, consumption, approximate digestibility (of biomass, N and C), %N and %C (in animal biomass and faeces).

Generally, grasshoppers preferred strongly fertilized grass, but we found differences between nymphs and adults and between the different species. Control grass was preferred to N grass only by *P. parallelus*. We found no differences in survival and consumption between the treatments. NPK grasshoppers digested least biomass, and the grasshoppers fed with NPK and N fertilized grass showed significantly increased body N concentration. We found no differences in %N in the plants, which might be explained by dilution effects through faster plant growth and heavier leaves. Increased N content in the insects is thus very likely explained by other foliar nutrients, which were not recorded. NPK fertilization led to increased N defecation, and control grasshoppers digested more N than those of the N treatment.

We demonstrated that fertilization of food plants can markedly influence the performance of grasshoppers, and that these insects preferred resources that received intensive N application. These widespread grasshoppers thus do not seem to be disadvantaged by increased N application in grasslands, which might be one reason for their tolerance of a variety of fertilization regimes.

Keywords: consumer-resource interaction, feeding ecology, insect, land use, Orthoptera, NPK fertilizer, stoichiometry

INTRODUCTION

Nutrient cycling in ecosystems is an important driver of inherent food web dynamics, community composition, and species diversity (Lindeman 1942, Elser et al. 2000). Nutrient-poor ecosystems provide opportunities for many different organisms, as resource limitation may prevent dominance of a few competitive species (Van Den Berg et al. 2011b). Highly diverse communities can thus result from resource limitation. Environments with high nutrient supply, in contrast, benefit single competitive species, which may lead to dominance of a few species (Wilson and Tilman 1991, Van Den Berg et al. 2011b) and competitive exclusion of many other species (Gazol et al. 2016).

Nutrient availability strongly affects plant productivity (LeBauer and Treseder 2008), which affects higher trophic levels including herbivores (Simons et al. 2014). Herbivores are dependent on the nutrient composition of their host plants (Joern et al. 2012), as they require an appropriate N-concentration in their food to grow and reproduce (Awmack and Leather 2002). It is known for a long time that nitrogen content is an important aspect of food plant quality and can directly change reproductive success of herbivorous insects (Dixon 1970). On average, C:N ratio in herbivorous insects is 5-10 times lower than in their potential food plants (Elser et al. 2000). Compared with predators, herbivores need to ingest substantially more food to keep their nitrogen concentration at a constant level (Simpson et al. 2015).

Plants intraspecifically vary in their nutrient content due to genetic but also environmental reasons (Güsewell and Koerselman 2002). Anthropogenic land use and particularly fertilizer application can have a strong influence on the variability of nutrients in potential food plants of herbivores (Klaus et al. 2011a). As herbivorous insects are directly affected by nutrient variation in their plant resources, they developed the ability to regulate their nutrient intake (Raubenheimer and Simpson 1993, Berner et al. 2005, Zhang et al. 2014). Regulation of nutrient intake requires internal mechanisms to measure the amount of ingested nutrients and to detect thresholds (Cease et al. 2016). When the threshold of a certain nutrient has been reached, feeding can be interrupted, excessively ingested nutrients can be excreted, or stored. Responses of herbivores thus can find expression in preference or performance. Essentially, preference and performance should be positively correlated, as it is expected that preferred food plants lead to optimized performance of consumers (Gripenberg et al. 2010).

When grasshoppers can choose between differently fertilized grasslands, they preferably occur on N-fertilized sites, whereas P does not seem to attract them (Loaiza et al. 2011). N has often be considered to be a limiting nutrient for grasshoppers (Joern and Behmer 1997, 1998, Fagan et al. 2002). Contradictorily, in north Asian grasslands nitrogen poor areas were preferred by a common grasshopper species (Cease et al. 2012). In this context the protein to carbohydrate ratio was of particular importance, that is, a high proportion of carbohydrates relative to protein was preferred and beneficial to grasshoppers concerning their survival. Here, preference and performance seem to correlate. This preference is suggested to be an evolutionary consequence of the grasshoppers'

specialization on grasses, which are protein poor by nature (Behmer 2009). For generalist grasshoppers, however, the preferred protein to carbohydrate ratio can be shifted to the opposite direction, that is, they need more proteins than carbohydrates (Behmer and Joern 2008, Behmer 2009). These ambiguous findings were clarified by the work of Behmer and Joern (2008), who found species-specific nutritional niches in grasshoppers, which enable these herbivores to coexist in the same habitats.

Nutrient regulation in herbivorous insects in general can occur in different ways. The common Asian grasshopper *Oedaleus asiaticus* (Bey-Bienko, 1941) reduces phosphorus absorption through increased excretion through its faeces (Zhang et al. 2014), or simply by food plant selection (Cease et al. 2012). Grasshopper nymphs are able to regulate their nutrient intake to gain an optimal growth (Raubenheimer and Simpson 1993). Apparently, grasshoppers are quite mobile, allowing them to select their food plants and feed on many different resources. This makes them insightful study organisms for many nutritional ecologists. As abundant grassland herbivores, they are main consumers of grass and forbs in European grasslands (Köhler et al. 1987) and can be found in nearly any grassland, even in anthropogenically influenced and urban areas.

With this study we aimed to examine the responses of the widespread European grasshopper species *Pseudochorthippus parallelus* (Zetterstedt, 1821), *Chorthippus dorsatus* (Zetterstedt, 1821), and *Chorthippus biguttulus* (Linnaeus, 1758) to different fertilization regimes of their food plants. We aimed to use a natural food resource, representing grasshopper responses to plant material that can be found by grasshoppers in different potential grasshopper habitats. We exposed the orchardgrass *Dactylis glomerata* (Linnaeus, 1753) plants to four different fertilization treatments: nitrogen (N), nitrogen-phosphorus-potassium (NPK), manure and unfertilized control. We tested preference of grasshopper nymphs and adults, and performance of adult grasshoppers in the different treatments. Performance experiments were supplemented with C/N analyses of the grasshoppers and their faeces to get insights into fertilization-mediated changes in nutrient utilization. We intended to answer four questions: (1) Do grasshoppers prefer grasses from a particular fertilization treatment? (2) Are there differences in preference between nymphs and adults or between grasshopper species? (3) Is fertilization beneficial to grasshoppers concerning their performance? (4) How does nitrogen fertilization influence food and nutrient utilization?

MATERIALS & METHODS

Fertilization treatment

One-year-old *D. glomerata* plants were fertilized three times within six weeks before the feeding experiments started. The experimental plots, which were located in the botanical garden of the University of Darmstadt (Germany), were exposed to four different fertilization treatments: nitrogen (N), nitrogen-phosphorus-potassium (NPK), cow manure (Manure) and unfertilized control (Control).

N plants were fertilized by ammonium nitrate solved in water, NPK plants by customary grainy compound-fertilizer (16% N, 7% P, 15% K, 3% Mg, 11% S; Beckmann & Brehm GmbH, Germany). Both treatments were fertilized with 30 g N per m^2 in total, portioned into three applications, to represent intensively managed grassland. Manure plants were fertilized with 5.6 g N per m^2 to reflect grassland of low management intensity. All four fertilization treatments received the same supply of water and weeding. Average dry mass of the differently fertilized grasses was estimated from leaves collected at two different sampling dates during the feeding experiment (n = 8 leaves per treatment). Plant height was detected before fertilization, two weeks after the first fertilizer application and two weeks after the second fertilizer application.

Grasshopper sampling

We sampled grasshoppers for preference experiments with nymphal and adult grasshoppers, and for performance experiments with nymphal grasshoppers. For the nymphal preference experiment, we sampled 60 nymphal Gomphocerinae (genera *Pseudochorthippus* and *Chorthippus*) grasshopper individuals in July 2016 from two sites differing in nutrient availability: 30 (15 females, 15 males) grasshoppers from unfertilized unmanaged grassland (site 1), and 30 (15 f., 15 m.) from managed grassland (site 2), both sites being located in Darmstadt, Germany. Site 2 was fertilized with approximately 1 kg/m^2 cow stable-manure and 0.8 kg /m^2 liquid cow-manure, which is equivalent to an approximate N input of 0.007 kg / m^2, and mown twice per year (information by local farmer). For the adult preference experiment, we sampled 90 adult grasshoppers from three species (*P. parallelus*, *C. dorsatus* and *C. biguttulus*) at equal sex ratios (15 f., 15 m.) in August 2016 from site 1.

The performance experiment was conducted with nymphal grasshoppers in July 2016 with 120 individuals (subfamily Gomphocerinae; 30 per fertilization treatment; equal sex ratios as far as possible) sampled from site 1.

Feeding experiments

Our preference and performance experiments were conducted under standardized climatic conditions in a climate chamber, which simulated an average German summer day from 2003 to 2013 (Rahlf 2013) with 10/14 hours day/night length, to reduce light-stress. Grasshoppers were kept separately in air-permeable plastic containers (diameter 50 mm, height 100 mm) and provided with grass leaves in moistened floral foam. For the preference experiments, we offered three evenly sized leaves of *D. glomerata* - one of each treatment group N, NPK and Control – to grasshoppers for 24 hours. Following the experiment, we quantified the leaf damage and released the grasshoppers at their site of origin. We quantified leaf damage by first assessing the difference in leaf area between intact and consumed leaf, and then by converting the area into consumed plant dry mass. Leaf area was measured from pixel area of scanned leaves using ImageJ 1.48v (Schneider et al. 2012), consumed leaf dry mass was measured by relating consumed leaf area to dry mass of reference leaves of known area. For our performance experiment, we provided grasshoppers *ad libitum* with one of the four differently

fertilized grasses (Control, Manure, N, NPK) for eleven days (afterwards named: N-/NPK-/Control-/Manure grasshoppers). Grasshopper faeces were collected and grass leaves were replaced every other day. Faeces dry-mass and dry body-mass of the grasshoppers were recorded at the end of the experiment.

After the performance experiment, C/N composition of the grasshoppers (without gut), food plants (three replicates of each treatment on five experimental days) and faeces was determined using gas chromatography (EA 1108, Carlo-Erba, Italy) with standard substances for accuracy (Hay powder BCR 129 by LGC Standards and Acetanilide by Hekatech).

Data analysis

Data analyses were conducted with R version 3.2.2 (R Core Team 2015). For analyses of preference experiments, we excluded grasshopper individuals that refused all grass leaves, leaving 50 nymph and 88 adult individuals. We used linear mixed effects modelling with the package 'lme4' (Bates et al. 2015). Ingested food dry-mass functioned as a proxy for preference of grasshopper individuals. To analyse overall feeding preference (including all grasshoppers of both trials), we fitted fertilization treatment, grasshopper age, grasshopper species, sex and body mass as predictors. To allow for repeated measures, grasshopper ID was fitted as random effect. We allowed for interactions between fertilization treatment and age or species, respectively. To predict nymphal feeding preference, we used the same model except for the factor age and any interactions, and used grasshopper origin as additional predictor. Adult and single species feeding preferences were analysed equally, without origin as factor. Effects of fertilization treatment and sex on grasshopper ingestion were tested by post-hoc Tukey's all-pair comparisons using the 'multcomp' package in R (Hothorn et al. 2008).

After exclusion of nine individuals that refused feeding, 111 individuals were left for analyses of performance and food utilization based on the following response variables: survival, consumption index (C.I.), approximate digestibility (A.D.) of food mass, %N and %C in body mass, %N and %C in faeces, approximate digestibility of N and C. We calculated C.I. for each individual, as $F/T \times A$, where F is the ingested dry mass of grass in mg, T the duration of the experiment in days (eleven days, except for some grasshoppers, which died before), and A the dry body-mass of the grasshopper at the end of the experiment (Waldbauer 1968). A.D. was defined as (F-C)/F, where C is the dry mass of faeces yielded during the whole experiment (Waldbauer 1968).

Survival of the grasshoppers in response to the fertilization treatment was analysed using cox proportional hazards regression modelling in the R package 'survival' (Therneau 2015) and post-hoc Tukey's all-pair comparisons. We analysed the consumption index C.I. in response to fertilization treatment and sex of the grasshoppers by linear modelling, using non-hierarchical factor order. The other variables were analysed in response to treatment and sex by linear mixed effects modelling using the package 'lme4' (Bates et al. 2015), to allow for random intercept between grasshoppers that survived the whole experiment and those that died before (14 individuals). We did not include survival

to the consumption model, as it is already part of our response variable (as variable T). Significance was tested with Satterthwaite approximation for degrees of freedom. The effects of fertilization treatment and date on plant height, specific leaf mass in mg/mm^2 and plant foliar %N were analysed by linear modelling. Multiple comparisons for significant treatment effects were tested post-hoc by Tukey's all-pair comparisons.

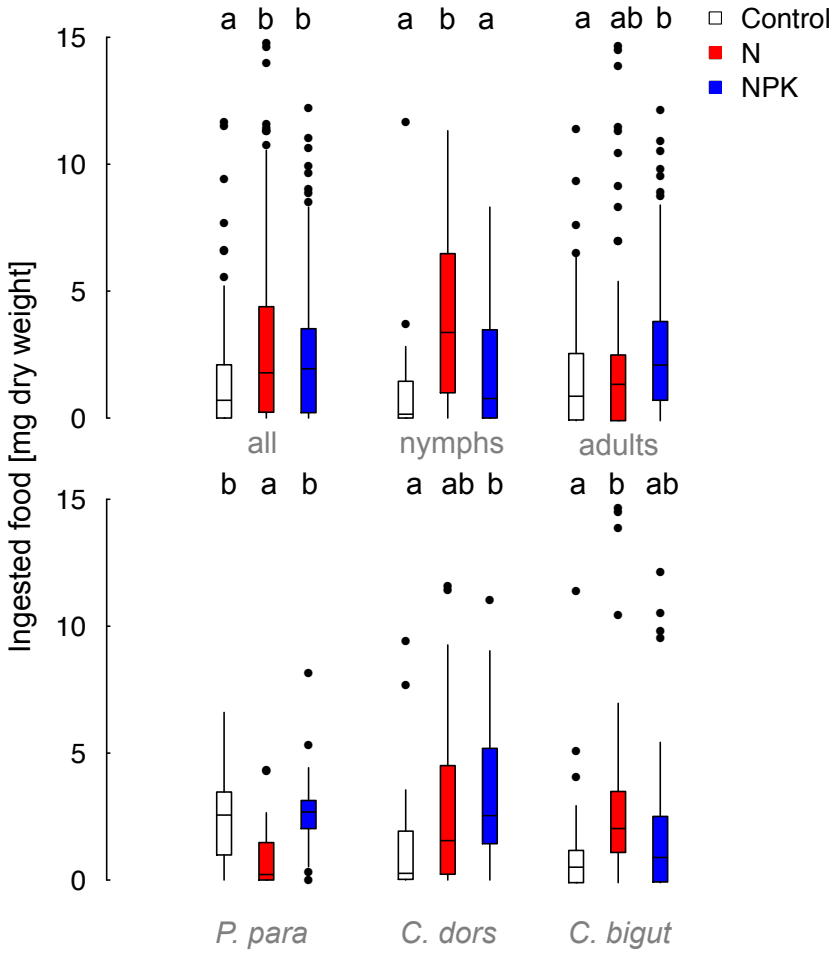

Figure 4.1: Feeding preference of grasshoppers for differently fertilized *Dactylis glomerata* leaves. We fed nymph and adult grasshoppers (first row: all nymph and adult grasshoppers, nymphs only, adults only) 24 hours with differently fertilized grass leaves (Control = unfertilized, N = Nitrogen fertilizer, NPK = full NPK fertilizer with additional micro-nutrients). All adults were determined to the species level (second row: *Pseudochorthippus parallelus*, *Chorthippus dorsatus*, *C. biguttulus*). We plotted ingested mg dry mass of leaf biomass as a proxy for preference. Lower case letters indicate significant differences following Tukey's post-hoc tests ($P < 0.05$).

RESULTS

Preference

Leaf ingestion of grasshoppers was strongly affected by the fertilization treatment as well as by sex of the grasshoppers (Fig. 4.1 "all"; Treatment: $F_{NumDF=,\ 2\ DenDF\ =\ 266} = 21.681$, $P < 0.001$; sex: $F_{1,132} = 22.701$, $P < 0.001$). Grasshoppers preferred N and NPK-fertilized grass to grass of the unfertilized Control-group (N – Control and NPK – Control: $P < 0.001$). Females ingested more food than males ($P < 0.001$) and individuals with undefined sex ($P < 0.001$). We found highly significant interactions between fertilization treatment and grasshopper age ($F_{2,266} = 23.861$, $P < 0.001$), and between

fertilization treatment and grasshopper species ($F_{6,266}$ = 5.26, P < 0.001). Grasshopper nymphs preferred N-fertilized grass to NPK and unfertilized grasses (Fig. 4.1 "nymphs"; N – Control and N – NPK: P < 0.001), while adult grasshoppers preferred NPK-fertilized grass to unfertilized grass (Fig. 4.1 "adults"; NPK – Control: P < 0.001). *Pseudochorthippus parallelus* individuals preferred NPK-fertilized and unfertilized grass to grass of the N treatment (Fig. 4.1 "*P.para*"; N – Control and N – NPK: P < 0.001). *Chorthippus dorsatus* preferred NPK to unfertilized grass (Fig. 4.1 "*C. dors*"; NPK – Control: P = 0.003), while *C. biguttulus* preferred N to unfertilized grass (Fig. 4.1 "*C. bigut*"; N – Control: P < 0.001, more detailed in supplementary material Table S 4.1, S 4.2).

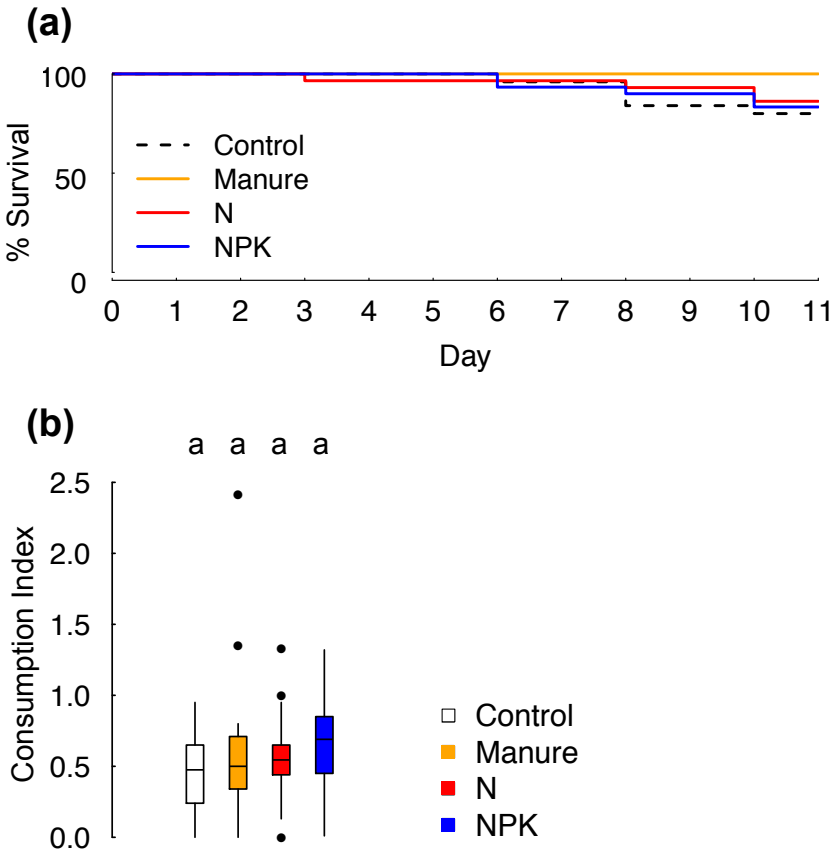

Figure 4.2: Performance of grasshoppers in the four fertilization treatments. Grasshoppers were fed for eleven days with unfertilized control-grass, manure-fertilized grass, N or NPK-fertilized grass (*Dactylis glomerata*). (a) Proportional survival of the grasshoppers during the experiment and (b) consumption index, which is ingested grass dry mass (mg) divided by the product of the grasshoppers' body dry mass (mg) and the number of days it survived. Lower case letters indicate significant differences between the treatments following Tukey's post-hoc tests (P < 0.05).

Performance

We found a significant effect of the fertilization treatment on grasshopper survival (Likelihood ratio test, df = 3, P = 0.033), but pairwise comparisons of grasshoppers from different treatments revealed no effects (see supplementary material Table S 4.4). All grasshoppers from the Control group survived, while survival was 80% for grasshoppers of the Manure group, 86% of the N group and 83% of the NPK group (Fig. 4.2a). Grasshoppers of the different treatment groups showed no differences in consumption (Fig. 4.2b; $F_{1,3}$ = 0.469, P = 0.705).

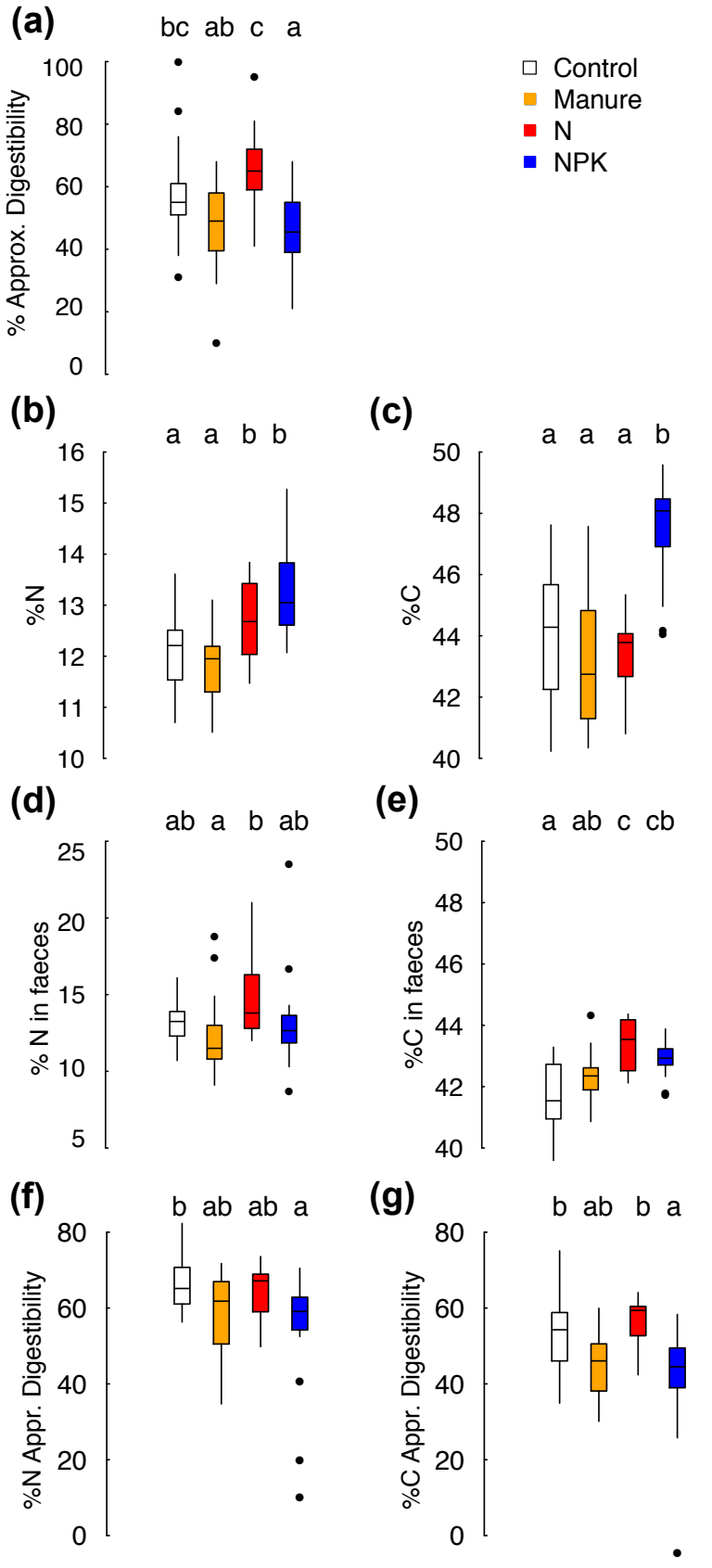

Figure 4.3: Nitrogen and carbon utilization of grasshoppers in the different fertilization treatments. (a) Approximate digestibility of food dry mass, (b) percentage N content and (c) C content of grasshopper biomass, (d) percentage N content and (e) percentage C content of grasshopper faeces, (f) percentage N and (g) C approximately digested by grasshoppers during the experiment. Lower case letters indicate differences between the treatments following Tukey's post-hoc tests ($P < 0.05$).

Nutrient and food utilization

Approximate digestibility differed significantly between treatments (Fig. 4.3a; $F_{NumDF= 3, DenDF = 105} = 11.42$, $P < 0.001$). NPK grasshoppers significantly digested less biomass than Control grasshoppers ($P = 0.002$) and N grasshoppers ($P < 0.001$). N Grasshoppers digested less biomass than Manure grasshoppers ($P < 0.001$). Digestibility differed also between the groups of determined and undetermined sexes ($F_{3,105} = 5.295$, $P = 0.006$).

The percentage N content of the grasshoppers differed significantly between the treatments (Fig. 4.3b; $F_{3,72.13} = 19.5$, $P < 0.001$). We found higher N contents in N and NPK grasshoppers than in Control and Manure grasshoppers (N – Control: $P = 0.04$; N – Manure: $P = 0.01$; NPK – Control/Manure: $P < 0.001$). Percentage C content of the grasshoppers also differed between the groups (Fig. 4.3c; $F_{3,73} = 30$, $P < 0.001$), as NPK grasshoppers had higher C contents than individuals from the three other treatment groups (all: $P < 0.001$).

N content of the faeces differed between the treatment groups (Fig. 4.3d; $F_{3,55.08} = 2.923$, $P = 0.016$), where N grasshoppers defecated more nitrogen than Manure grasshoppers ($P = 0.02$). C content of the faeces also differed between the treatment groups (Fig. 4.3e; $F_{3,56} = 9.847$, $P < 0.001$), where N grasshoppers defecated more C than Control ($P < 0.001$) and Manure grasshoppers ($P < 0.001$). NPK grasshoppers defecated more C than Manure grasshoppers ($P < 0.001$).

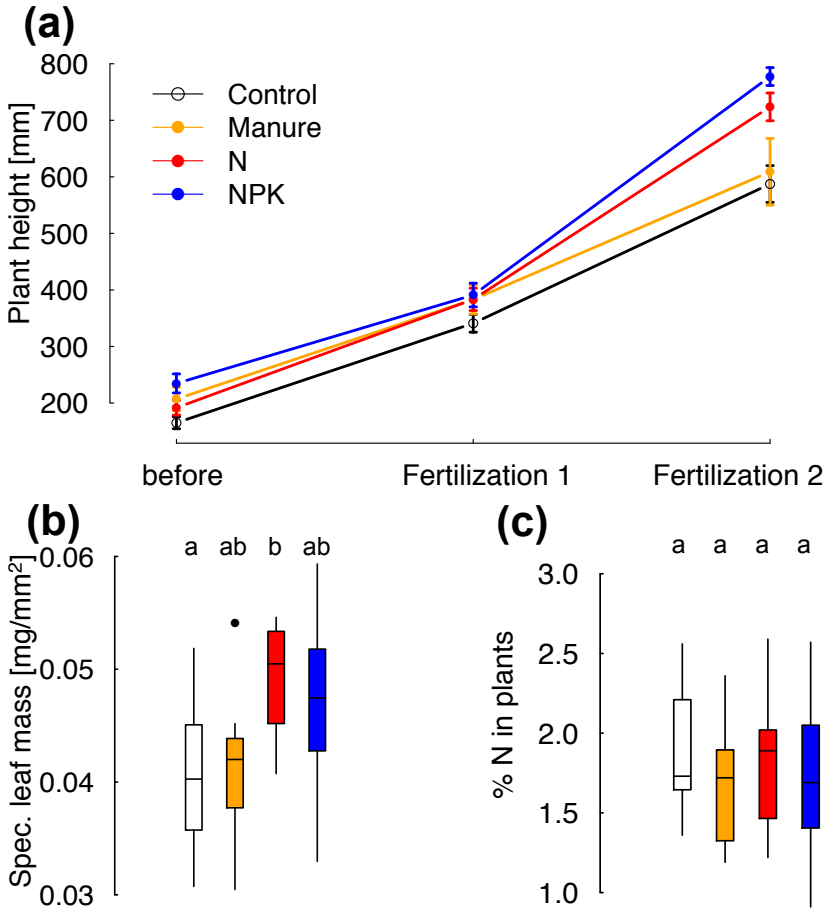

Figure 4.4: Plant responses to different fertilization treatments. (a) Height of differently fertilized *Dactylis glomerata* plants before first fertilization, two weeks after first (Fertilization 1), and two weeks after second fertilization (Fertilization 2; n = 165 random leaves measured in total); (b) specific leaf mass of differently treated plants (n = 32); (c) percentage N concentration in the plants during the grasshopper performance experiment (n = 60).

We found significant effects of the fertilization treatment on approximate N digestibility (Fig 4.3f; $F_{3,55.128}$ = 3.296, P = 0.027). N digestibility was higher in Control grasshoppers than in NPK grasshoppers (P = 0.02). Also C digestibility significantly responded to the fertilization treatment (Fig 4.3g; $F_{3,56}$ = 4.762, P = 0.005), where NPK grasshoppers digested less C than N (P = 0.034) and Control grasshoppers (P = 0.009).

Dactylis glomerata height differed between the treatment groups (Fig. 4.4a; $F_{1,3}$ = 11.714, P < 0.001). Plants that were treated with NPK fertilizer were taller than plants of the Control (P < 0.001) and Manure group (P = 0.04). Specific leaf mass was also significantly affected by fertilization treatment (Fig. 4.4b; $F_{1,3}$ = 4.094, P = 0.016), with N-fertilized plants showing heavier leaves than unfertilized Control-plants (P = 0.033). In contrast, plant nitrogen-content was not affected by the fertilization treatment (Fig. 4.4c; $F_{1,3}$ = 1.127, P = 0.346) and by the day of leaf collection ($F_{1,3}$ = 2.326, P = 0.133; see supplementary material Table S 4.3 for detailed model results on nutrient utilization of grasshoppers and plants and Table S 4.4 for results of multiple comparisons).

DISCUSSION

Our feeding experiments revealed that grasshoppers generally preferred grass that was fertilized with N and NPK fertilizer compared to unfertilized grass. However, the effects of fertilization differed between nymphal and adult grasshoppers, and between different grasshopper species. We found no marked differences in survival and consumption of the grasshoppers in the performance experiment, for which grasshoppers were held on each one of the four differently fertilized resources. Grasshoppers that were held on NPK-fertilized grass digested least biomass, nitrogen, and carbon. Strong fertilization increased nitrogen content of the animals after a feeding period of eleven days. This study demonstrates that grasshoppers respond to fertilization via resource preferences, and changes in performance and food utilization.

Preference

The grasshopper's dietary preference for fertilized food plants demonstrates that these herbivores can distinguish between plants from environments differing in nutrient availability. Grasshoppers have the ability to decide between food resources through chemical receptors for amino acids and carbohydrates on their mouthparts (Chapman 2003), and are capable of regulating their diet intake in terms of carbohydrate to protein ratio (Simpson and Simpson 1992, Behmer 2009, Cease et al. 2012). The intake of other nutrients can also be regulated by post-ingestive feedbacks, like for essential sterols (Behmer et al. 1999).

In American tall-grass prairies, grasshopper densities and leaf damage were markedly higher in fertilized than in unfertilized sites (Loaiza et al. 2011). In contrast, grasshoppers of the species *Oedalus asiaticus* preferred food plants with low N content (Cease et al. 2012). The preference for

nitrogen-rich food can differ between available grass species, which was reported for the common North American range grasshopper *Phoetaliotes nebrascensis*. While the grass *Andropogon scoparius* was preferred under high nitrogen fertilization, the grass *A. hallii* was preferred under low fertilization intensity (Joern and Alward 1988). We found no studies, where this issue was tested for *Dactylis glomerata*, but as our study assumes this plant is more attractive when it is fertilized. We found differences between nymphs and adults, and also between the different grasshopper species, our study suggests that not only the grass species, but also grasshopper characteristics predict grasshopper preference.

Nymphal grasshoppers can have other nutrient requirements than adults, as they need specific substances for development and moulting (Sterner and Elser 2002). Changes in nutrient composition may also occur between nymphs of different instars, which was reported for *Schistocerca americana* nymphs that were reared on the same resource (Boswell et al. 2008). Early instars showed higher concentrations of N, Na, Ca, Mg, Mn, and Cu; these high concentrations usually decreased after the second instar. This study also presumed that high elemental concentrations function as reserves, which are provided by female grasshoppers to support growth of their progeny.

We found the three grasshopper species to prefer plants from different fertilization treatments. Except for *P. parallelus*, fertilized plants were preferred to unfertilized ones. There are reports describing species-specific nutritional niches of grasshoppers, which are reflected in their dissimilar carbohydrate to protein intake, even if the insects share the same food plants (Behmer and Joern 2008). Another predictor of preferred nutrient composition in food plants can be the grasshoppers' feeding guild. Grass feeders, for example, are more abundant on sites that are rich in N, P, Mg and Na (Joern et al. 2012).

We are aware of potential other factors that we did not record in our study, and our model indicates that food choice was not only explained by the fertilization treatment. Firstly, we did not record parasitism of grasshoppers, although nutrient regulation can be directly or indirectly altered by parasitism (Behmer 2009). Secondly, nutrient intake is differently regulated in the different developmental stages of grasshoppers (Raubenheimer and Simpson 1993), which we assume to be an important predictor of food choice. We distinguished between nymphs and adults, but there are different nymphal instars and moulting conditions, which was not considered by this classification. Thirdly, nutrient requirement is dependent on the reproductive status of females (Awmack and Leather 2002). Fourthly, the micronutrient composition of food plants may vary intraspecifically and has been revealed to influence grasshopper assemblages (Joern et al. 2012), which can be considered as a preference to plant communities with specific nutrient availability.

Performance, nutrient utilization and plant nutrients

The survival and the consumption of the studied grasshoppers were not markedly affected by the fertilization treatments. Disaccording, nutrient-rich diet have been recorded to decrease the survival of

grasshoppers (Joern and Behmer 1998). Consumption of grasshoppers on low quality food (less nutrients), was higher than on food of higher quality (Fielding and Defoliart 2007), which we could not confirm with our experiment. One would expect grasshoppers to handle possible nutrient deficiencies with compensatory feeding, like it has been addressed by previous studies (Raubenheimer and Simpson 1993, Berner et al. 2005).

However, we found other responses of grasshoppers to the fertilization treatments, as grasshoppers feeding on strongly fertilized grass digested more biomass, increased their percentage body-N and C, increased defecation of N and C, and decreased N digestibility. Animals, which feed only on one resource, like in our performance experiment, can compensate excess of one nutrient by excretion or by stopping the intake.

The fact that the studied grasshoppers directly responded to N application with increased body N-content, whereas no changes in N-content of plants were observed calls for further inquiry. The grasshoppers of the preference experiment clearly preferred fertilized food plants. This indicates that plants differed in traits that were detectable for grasshoppers but not reflected by our measurements of C/N content. Fertilizer application has been shown to lead to increased foliar N and P contents in some plants (Cui et al. 2010a, Loaiza et al. 2011, Klaus et al. 2011a), and to increase productivity (Craine et al. 2008, Faust et al. 2012). On the other hand, increased growth rate of plants may also dilute nitrogen content in leaf material (Imo and Timmer 1997) and thus impede detection of increased nitrogen levels. As strongly fertilized plants in our experiment (N and NPK treatment) were significantly taller than the control or weakly fertilized plants (Manure treatment), dilution effects may thus help to explain a lack of increasing N content as observed in our fertilization treatments. Besides the unmeasured factors we discussed above, also P content has been shown to alter grasshopper performance (Cease et al. 2016), even though foliar P-content had no influence on preference of grasshoppers (Loaiza et al. 2011). In addition, there is evidence that mechanical plant-traits (like leave toughness) influence the feeding behaviour of herbivorous insects (Clissold et al. 2009, Caldwell et al. 2016), and are expected to be even more substantial than secondary plant metabolites (Carmona et al. 2011). We measured higher specific leaf-mass for fertilized plants, indicating that those leaves showed more mechanical strength than the other ones. Contradictorily, stronger leaves would be expected to be avoided by herbivores and not preferred.

Though *Dactylis glomerata* is an important food plant, there are few current studies dealing with its compositional response to fertilization. Productivity increased with nitrogen fertilization in *Dactylis glomerata* (Donohue et al. 1973, Malzer and Schoper 1984, Bittman et al. 2004a). Plants grew strongest right after the first N application and cut, having an intermediate growth in between and increased again in the end of the growing season (Bittman et al. 2004a). Donohue et al. (1973) reported increased N content in the plants, the other studies showed that protein content increased with increasing nitrogen application. An increase of foliar protein content due to N fertilization has also been reported in north Asian grasses (Cease et al. 2012). Our *Dactylis glomerata* plants were sown one

year before the feeding experiments started and were already mown twice; our fertilizer was applied in three portions. We observed visible differences (darker colour, faster growth, more biomass in strongly fertilized grasses) between the grass treatments, which indicate additional responses of the grass to fertilizer application. With our decision to use an authentic and natural food resource, we ceased the opportunity to define the exact nutrient composition of provided food and tolerate variation in nutrient composition within treatments. It is likely that our plants differed in their protein content, as we reported differences in the grasshoppers' responses to grass fertilization. N enrichment in plants can decrease grasshopper performance (survival, size, growth rate), increased developmental (Cease et al. 2012), and have negative effects in egg production (Joern and Behmer 1998).

Nutritional-ecology studies showed that the analysis of nutrient intake by locusts is complex and follows a certain geometry, which is time dependent (Simpson and Raubenheimer 1993). The optimal feeding status is dependent on the intake of several nutrients, for which different feeding intervals are needed, e.g. when a peak of one nutrient has been reached, the amount of ingestion is reduced for a while until threshold is reached and ingestion starts again. Feeding requirement is not a static system, but is dependent on many factors.

Conclusions

The current study reports the preference of common European grasshoppers for strongly fertilized grasses and thus their ability to choose between fertilization treatments. Feeding the grasshoppers with strongly fertilized grass led to higher body N-content and increased N defecation. Our findings demonstrate that feeding preferences are species specific, which fits into the current context of knowledge (Behmer and Joern 2008), and that animal responses to fertilization (N and NPK) are not necessarily explained by N content of the resource. Knowing the interactions between resources and their consumers is a central issue in understanding the links that form networks and thus ecosystems with their inhabiting communities. Relating the dynamics of feeding decisions and responses to resource quality, our study may motivate researchers to continue with experiments that integrate the complexity of nutrient regulation and natural resource supply.

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GENERAL DISCUSSION

The aim of this thesis was to understand how changing environmental conditions influence herbivorous insects and to shed light on the complex relationships between habitats and their communities with additional consideration of single species. The three research chapters give insights into the effects of anthropogenic land-use on ecosystem components and their way of dealing with land-use consequences. In the following I will discuss the results of the research chapters with reference to the three main objectives that were presented in the introduction: 1) understanding land-use effects on communities, 2) single species, and 3) individual effects of fertilization on herbivorous insects.

Understanding land-use effects on communities

Loss of species and density decrease

Land-use change is associated with loss of diversity and this definitely applies to herbivorous insects. As reported in the chapters I and II, declines in diversity can be observed for the two important herbivorous groups Orthoptera (grasshoppers and long-horned grasshoppers) and Auchenorrhyncha (plant- and leafhoppers). Both groups suffered a loss in species diversity with increased compound land-use intensity (LUI), and also with increased fertilization and mowing intensity. Orthoptera diversity additionally decreased with increasing grazing intensity (see Table 5.1).

For Orthoptera this trend is likely to be caused by the loss of suitable habitats and micro conditions, whereas for plant- and leafhoppers it may be driven by plant-diversity loss. Orthoptera are more generalist in dietary choice than are plant- and leafhoppers, and feed mainly on grasses (Ingrisch and Köhler 1998). As grasses benefit from fertilization through higher competitive ability in nutrient-rich environments than forbs (Garratt et al. 2010, Gaujour et al. 2012), there must be other causes for orthopteran diversity-decline than food-plant loss. Many Orthoptera species are dependent on particular environmental conditions, such as dry and warm climate, which can only be ensured by open habitats with loose vegetation. Some species are dependent on open soil spaces, vegetation height or long periods without mowing to ensure the hatching of eggs that are laid into foliar material (Ingrisch and Köhler 1998, Weiss et al. 2012). The listed conditions are all only feasible by a reduction of management intensity and can more likely be found in calcareous or sandy low-nutrient grasslands (Weiss et al. 2012). As fertilization increases plant productivity (Garratt et al. 2010, Gaujour et al. 2012, Socher et al. 2012), the availability of open spaces is reduced by nutrient application. In this context, one might expect that mowing or grazing is beneficial to Orthoptera as it opens the vegetation structure. However, the negative impacts of mowing through the physical damage and killing or the rapid changes in food and shelter availability (Humbert et al. 2009, 2010) outweigh potential positive effects. The same might be relevant for grazing by large animals, which can be an adverse factor in disturbance (Kruess and Tscharntke 2002).

Interestingly, abundance of Orthoptera did not decline with increasing LUI and fertilization. Abundance is particularly maintained by single competitive species that profit from increased grass productivity through human practices. These results corroborate the findings of another large-scale study, where herbivore species richness is negatively and abundance is positively correlated with plant-tissue nitrogen (Haddad et al. 2000). The increase of plant-tissue nitrogen with fertilization has been reported frequently (Cui et al. 2010b, Loaiza et al. 2011, Klaus et al. 2011b).

Plant- and leafhopper communities also depend on a diverse flora as this insect group includes a large proportion of dietary specialists. Hence, the loss of plant species means the loss of monophagous or oligophagous species that depend on these hosts. The results of chapter II corroborate this assumption, as monophagous species declined and polyphagous species increased with increasing land-use intensity. However, plant-diversity mediated effects did not by themselves explain the impact of land use on Auchenorrhyncha communities, as Auchenorrhyncha density also declined with increasing land-use intensity. A possible cause might be the dependency of Auchenorrhyncha diversity on diverse habitat types, including all gradations from arid to wetland. Increasing land-use intensity leads to homogenization of landscapes (Hendrickx et al. 2007, Gámez-Virués et al. 2015) and thus impedes the availability of various habitat types. Furthermore, generalist Auchenorrhyncha-species might be less competitive (within Auchenorrhyncha) than those in Orthoptera and might not be able to fill the space (in terms of density) that their monophagous congeners left.

An important difference that should not be neglected is that Orthoptera and Auchenorrhyncha significantly differ in their feeding guild: Orthoptera are folivores, Auchenorrhyncha are sap suckers. This fact makes it interesting to consider both groups separately, as they do not compete for food resources. The difference in feeding mode leads also to different plant traits that both groups might be affected by. While for leaf-chewing insects mechanical traits (e.g. epidermal silica crystals in graminoids) are of greater importance, for sap-sucking insects it might be secondary plant compounds (Nickel 2003). The similarity of both groups is their high mobility. In most cases they have the ability to move by hopping, flying and walking. One would think that such features make it rather easy for these insect-herbivores to flee from disturbance sources, but they show high susceptibility to intensive land-use, according to this thesis.

Homogenization

In chapter II an increased trend to within-site homogenization of plant- and leafhopper communities with increasing LUI has been found. Decreasing β-diversity reflects that species richness within sites reach similar levels as total-site species richness. In other words, with an increase of land-use intensity we cannot find small-scale differences within grasslands, but rather find the same community over larger areas. This might be promoted by synchronous management of large areas, which is often the case, as large farms increasingly replace small agricultural holdings. What here is reported on a small-scale can be also found in large-scale studies. In the same studied grassland sites as used here, multi-taxonomical homogenizations among the sites have been reported before (Gossner et al. 2016).

Landscape simplification not only drives taxonomical homogenization, but also functional homogenization (Gámez-Virués et al. 2015), which is even more critical in the view of 'functional redundancy'. Functional redundant species share the same function in an ecosystem, and the balance of these functions is supposed to be of greater importance than species diversity *per se* (Lawton and Brown 1994). The loss of functional diversity can result in decreased ecosystem reliability (Naeem 1998, Olden et al. 2004), e.g. an increased vulnerability to global environmental events (Olden et al. 2004), which is particularly worrying in the context of climate change.

Understanding land-use effects on single species

The investigation on the species level provided more precise insights into the susceptibility of herbivorous grassland-insects to intensive land-use. Without exception we found more losers than winners of strong land-use intensity. This trend was applicable to compound LUI and the single management types fertilization, mowing and grazing, and was applicable to both Orthoptera and Auchenorrhyncha (see Table 5.1).

In summary, Orthoptera were more susceptible to high land-use intensity than Auchenorrhyncha on the species level. Orthopterans were most impaired by fertilization, followed by mowing and grazing, while Auchenorrhyncha were most impaired by mowing, followed by fertilization and grazing. The strong susceptibility of orthopterans to fertilization corroborates the findings on the community level: massive changes in vegetation structure and microclimate, which adversely affect many species, lead to decline in species diversity. Auchenorrhyncha, which 'only' had 15% losers of strong fertilization, had similar declines in diversity and additionally in density on the community level. Zooming into the whole species pool, it is conspicuous that half of the Auchenorrhyncha species only occurred on unfertilized sites: these species contribute to diversity declines on the whole-community level.

Both Orthoptera and Auchenorrhyncha had 28% losers of high mowing intensity. On the species level as well as on the community level, mowing is the management type that has most consistent negative impacts on different groups of herbivorous grassland-insects. The harsh procedure of cutting meadows might be problematic because of actions that include physical damage or rapid degradation and change of the current habitat (discussed in detail in research chapters I and II), which might have the same adverse effects across groups.

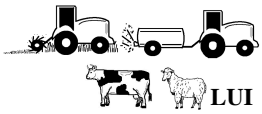
Grazing was for Orthoptera the least detrimental impact; nevertheless it was negative on the species as well as on the community level. Auchenorrhyncha in turn, showed only weak responses to the grazing level, both in the single-species and community view. Livestock grazing has been found to be more beneficial to Orthoptera diversity than mowing in extensively managed German grasslands (Weiss et al. 2012), which we could confirm in the single-species but not in the community analysis.

The point that was made in the community discussion that designated a few benefiting generalist species could be confirmed by findings of chapter II. The few plant- and leafhopper species that had very high total abundances and/or widespread occurrences were the same ones that had their broader

niches in a range of intensive LUI, fertilization or mowing. However, once again no coherence between abundance/site-occurrence and niche position could be found for grazing.

Table 5.1: Comprehensive view of the findings of chapter I and II. The major trends of compound land-use intensity (LUI), fertilization, mowing and grazing intensity on diversity and density on plant- and leafhoppers (1st row) and Orthoptera (2nd row) are illustrated. The lower part refers to the percentage of losers and winners of land-use intensity according to the niche model.

In a nutshell

	 LUI	 Fertilization	 Mowing	 Grazing
Diversity				
	decline	decline	decline	no effect
	decline	decline	decline	decline
Density				
	decline	decline	decline	no effect
	no effect	no effect	decline	decline
Single species-level				
	34% losers 6% winners	15% losers 6% winners	28% losers 9% winners	9% losers 5% winners
	51% losers 10% winners	31% losers no winners	28% losers 10% winners	14% losers 10% winners

Understanding the individual effects of fertilization on herbivores

Preference of the grasshoppers

As an extension to the study of land-use-effects on herbivorous insects, this thesis incorporates another aspect to cover the resource-consumer relationship: a controlled laboratory-experiment to test direct responses of consumers (grasshoppers) to fertilized plants. In general, chapter III demonstrated that grasshoppers prefer strongly fertilized to weakly or unfertilized grass, however, there were differences between nymphs and adults, and among different species.

The preferential differences between grasshopper species complement our knowledge about species-specific nutrient niches (Behmer and Joern 2008). These niches are proposed to be results from the different requirements in protein to carbohydrate ratio of single species. As N or NPK fertilized grasses were the most preferred resource in the choice experiment, a trend to high protein to carbohydrate ratio can be expected in the examined grasshoppers. Provided, of course, that nitrogen (N) application increased protein content of plants as demonstrated in previous studies (Malzer and Schoper 1984, Bittman et al. 2004b, Cease et al. 2012). It is conceivable that not only macronutrients such as proteins and carbohydrates play important roles in feeding decisions of herbivores, but also

micronutrients (e.g. minerals, vitamins) and water. As nymphal individuals are still in the growth phase and undergo several moultings they have different requirements than adults. Therefore, specific amino-acids that are essential for cuticle production are needed and preferred by nymphal grasshoppers (Chown and Nicolson 2004). The knowledge about the different needs in lipid and sugar nutrition of larval and adult insects is well established (Friend 1958).

It is very likely that not only nutritional stimuli in the resources, but also mechanical (Caldwell et al. 2016) or visible plant-traits play a role in the feeding decisions made by herbivorous insects. High nutrient availability might lead to differences in leaf toughness, thickness and colour. In chapter III, grass plants responded to increased fertilization with heavier leaves and higher plants, even though nitrogen content did not differ between the plant treatments. Possibly the grasshoppers were able to distinguish these traits and were potentially influenced by them.

The three grasshopper species considered in the feeding experiments were rather common and widespread species. The niche analysis in chapter I characterized both *Pseudochorthippus parallelus* (therein *Chorthippus parallelus*) and *Chorthippus biguttulus* as opportunists; *C. dorsatus* was characterized as a loser of intensive fertilization. Hence, the obvious assumption is that opportunists are less selective and losers are more selective concerning their resources. If preference of the food resource is related to better performance on this resource (Gripenberg et al. 2010), this assumption is justified. The grasshoppers of chapter I, however, had no choice between different fertilization regimes, which makes chapter I and III hardly linkable.

Food and nutrient utilization

In a no-choice experiment (chapter III), four treatment groups of grasshoppers were each fed on one of the four differently fertilized grasses for eleven days. No differences in consumption were found among treatment groups, even though one would expect higher consumption on low nutrient resources, as compensatory feeding is a common way to regulate nutrients in grasshoppers (Raubenheimer and Simpson 1993, Chown and Nicolson 2004, Berner et al. 2005). Survival also did not differ among the dietary treatments, showing that fertilization is not directly harmful to grasshoppers through potential changes in food-plant quality. This might be different in rare grasshopper species that disappeared with increasing fertilization intensity (chapter I) and were not considered in the feeding experiments. Synthesising the chapters I and III, the hazard of fertilization for grasshoppers is rather indirect via plant-diversity and vegetation-structure changes, instead of directly from changes in leaf quality or nutrient content.

After the feeding period of eleven days the examined grasshoppers of the N and NPK treatments (highly fertilized plants) had an elevated N concentration in their body mass. Potential increases of protein content in the plants or the availability of better metabolisable substances might explain increased nitrogen concentration in the grasshoppers.

Grasshoppers of the N treatment had highest N concentrations and highest N defecation, indicating an

oversupply of N for this group, which is compensated by excretion of surplus N. This is an indication of post-ingestive rather than pre-ingestive nutrient regulation, which is proposed by previous studies (Chown and Nicolson 2004 and references therein). However, it is rather complex to interpret the conflicting findings that, firstly, strongly fertilized plants did not contain more N, secondly, grasshoppers did not differ in consumption among the treatments and, thirdly, the grasshoppers still have higher N contents in their body mass and faeces. Extensive research and more observational data are needed to fully comprehend the processes behind the findings of chapter III.

Control grasshoppers (fed with unfertilized grass) digested more N, C and biomass than the NPK grasshoppers. The potential nutrient deficiency of this treatment group has been compensated by different nutrient utilization. The findings of chapter III suggest that feeding decisions and nutrient utilization are a dynamic system, which are highly adaptable to current changes in nutrient availability.

Synthesis and applicability

In conclusion, intensified land-use is harmful for the diversity of herbivorous insects. The intensive sampling and the large scale that has been examined shed light into management effects on Central European grassland-communities. The trends this thesis elucidates, match with the global context in which biodiversity loss and community homogenization are reported with increasing land-use intensity, and land-use change is designated as a major driver of diversity impoverishment. Thereby, the quality of biodiversity can be defined by functional, phylogenetic, and genetic diversity, by the ratio of species which are associated with humans or not, by rare versus common species and by specialists versus generalists (McGill et al. 2015). Of course, grassland management represents a rather harmless land-use, compared to arable farming that additionally involves pesticide application and the reduction of plant species richness to (preferably) one species (Stoate et al. 2001). Nevertheless, even grassland management leads to notable diversity loss, which is rather worrying.

To improve the situation for biodiversity of global ecosystems, people have to rethink land use. Beside the findings of this thesis, the scientific literature provides many suggestions that can help to obtain benefits for the environment and humanity. Needless to say, land-use itself cannot be abandoned, but management changes such as rotational mowing and grazing, leaving uncut patches on meadows (Rook and Tallowin 2003, Bilotta et al. 2007, Gardiner and Hassall 2009, Humbert et al. 2009, 2009, 2012, Cizek et al. 2012), yearly variation in intensity and methods of management (Allan et al. 2014), protection of semi-natural habitats and suitable habitat corridors (Gilbert et al. 1998, Hendrickx et al. 2007, Gaujour et al. 2012, Mitchell et al. 2014), and agri-environmental schemes such as flower strips or hedgerows (Kleijn et al. 2006, 2009) can improve biodiversity in various ways.

What has been demonstrated is that community and species responses differ and thus a multi-level approach gives important insights into the complexity and fragility of ecosystems. The specification of land-use niches of single species makes it easier to predict how communities will look like under different land-use regimes. The niche analysis does not incorporate interspecific interactions such as

competition, but the benefit of the niche analysis is that it is sensitive to rare species, which is not the case in community or compositional analyses. In summary the findings of this thesis show that research on single species responses can give answers that are applicable to the understanding of community responses, and broadening our conceptual view to diverse aspects is worthwhile.

My thesis complements the current knowledge on the harmfulness of land-use change and reflects the importance to concentrate on different ecosystem-levels and to apply different analytical approaches to understand responses to environmental gradients. As I drew attention to communities and single species, I demonstrated an opportunity to gain a broad insight into the complex and various effects of land-use on biodiversity.

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SUPPLEMENTARY MATERIAL

Supplementary material can be found on an attached Compact Disc

Supplementary material for chapter I

Supplementary material for chapter II

Supplementary material for chapter III

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Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit entsprechend den Regeln guter wissenschaftlicher Praxis selbstständig und ohne unzulässige Hilfe Dritter angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommenen Gedanken sowie sämtliche von Anderen direkt oder indirekt übernommenen Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher bei keiner anderen Hochschule zu Prüfungszwecken eingereicht.

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